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THE INFLUENCE OF HABITAT FRAGMENTATION ON POPULATION STABILITY OF COLORADO RIVER CUTHROAT TROUT IN UINTA MOUNTAIN STREAMS

by: C.P.Hawkins,J.L.Kershner &T.A.Crowl

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The Influence of Habitat Fragmentation on Population Stability of Colorado River Cutthroat Trout in Uinta Mountain Streams

Final Report

Submitted to:

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U.S.D.A Forest Service
Boise, Idaho

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PREFACE

This document is intended to fulfill the obligation of a final report associated with our study on "**The Influence of Habitat Fragmentation on Population Stability of Colorado River Cutthroat Trout in Uinta Mountain Streams**". The scientific objectives of this study were to:

1. Determine the current population sizes of Colorado River cutthroat trout in isolated subbasin fragments in the Uinta Mountains.

2. Determine whether risks of extinction are likely different across the subbasin fragments

3. Determine whether analyses using population size structure provide additional information than more traditional habitat modeling approaches

4. Determine the relationships between available habitat area, population density and population structure.

5. Determine whether exotic species, such as brook trout, affect the population dynamics of Colorado River cutthroat trout.

This document has four chapters, each dealing specifically with one or more of the

objectives. Chapter 1, entitled 'Habitat relationships of Colorado River cutthroat trout in fragmented stream ecosystems of the Uinta Mountains, Utah' will be submitted to the Transactions of the American Fisheries Society and deals explicitly with objectives 1 and 4 and implicitly with objective 2. The second chapter entitled, 'Assessing population attributes and habitat requirements of a size-structured Colorado River cutthroat population in fragmented watersheds: a case study' will be submitted to Conservation Biology and deals specifically with objective 3 and generally with objectives 1,2 and 4. The third chapter, 'A comparison of population, habitat, and genetic characteristics of Colorado River cutthroat trout in wilderness and nonwilderness streams in the Uinta Mountains' will be submitted to Conservation Biology and addresses objectives 1, 2, 4 and 5 (discussion of rainbow hybridization). Chapter four, entitled 'Competitive interactions between a native and exotic trout species in high mountain streams' directly addresses objective 5 and will be submitted to Ecology. Chapters 1 and 4 are direct results of Master's Theses by Dona Horan and Heather Thomas, respectively. Chapter 3 comprises part of a Master's Thesis by Cathy Bishoff.

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This work would not have been accomplished without the dedicated efforts put forth by a myriad of undergraduate technicians, too numerous to list. Chuck Hawkins provided clerical support.

CHAPTER I

HABITAT RELATIONSHIPS OF COLORADO RIVER CUTTHROAT TROUT IN FRAGMENTED STREAM ECOSYSTEMS OF THE UINTA MOUNTAINS, UTAH

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Abstract

Habitat degradation has fragmented and reduced the complexity of streams on the northslope of the Uinta Mountains. Fragmentation has reduced the historic range of Colorado River cutthroat trout *Oncorhynchus clarki pleuriticus*, has isolated populations, and presumably increased this subspecies' risk of extinction. In addition, land use activities have altered habitat conditions in many mountain streams including the complexity of habitats present in streams. This study was designed to determine if variation among locations in densities and size structure of Colorado River cutthroat trout were associated with differences in habitat conditions and complexity.

We sampled 88 - 100 m reaches in 4 fragmented stream basins in the Uinta Mountains of northeast Utah that differed in size. In each basin we quantified habitat conditions (basin area and stream length; channel depth, width, and residual pool depth; amount of undercut banks, pool habitat, and large woody debris; substrate size; and hydraulic retention time) and densities of juvenile and adult cutthroat trout. A habitat complexity index was calculated from a subset of the habitat data. Data were analyzed at 2 spatial scales (basin and reach) by regression analyses.

Adult trout densities varied between 0.0 and 17.7 fish / 100 m^2 and juvenile trout densities varied between 0.0 and 32.9 fish / 100 m^2 among reaches. Trout size (individual mass) varied 4.8- and 66.7-fold across reaches for adults and juveniles respectively. At this spatial scale adult density was most strongly related to elevation (+), the amount of undercut banks (+), mean substrate size (+), mean depth (-), and

large woody debris (-). Juvenile density was most strongly related to mean residual pool depth (-), mean channel width (-), and large woody debris (+). Individual mass of adult trout was related to residual pool depths (+), elevation (+), and mean channel depth (+), whereas individual mass of juvenile trout was related only to channel width (+). However, the strength and significance of these relationships varied among basins.

Total estimated population size varied almost 10-fold among basins, and abundances and mean individual sizes of adult and juvenile trout were related to different habitat features. Population sizes of adults, juveniles, and total fish were strongly and positively related to basin size. Adult density, percent of the population as adults, and mean length and weight of both juveniles and adults were also positively related to basin size, but juvenile population size and juvenile density were not. Adult trout density was positively related to undercut banks, pools, and mean depth, whereas juvenile trout density was positively related to large woody debris and negatively related to mean depth. Similar correlations existed between habitat complexity and both trout abundance and size, but habitat complexity and basin size were correlated with one another so the effects of the 2 factors could not be isolated.

Keywords: trout, habitat, complexity, fragmentation

INTRODUCTION

Historically, the Colorado River cutthroat trout *Oncorhynchus clarki pleuriticus* was widely distributed among the cold-water tributaries of the Green River and upper Colorado River basins (Behnke and Benson 1980). Now, it is thought to occupy less than 1% of its historical range (Behnke 1979), and federal and state agencies have responded to the decline of this subspecies of cutthroat trout by providing it with special status. The Colorado River cutthroat trout (hereafter CRCT) was classified as a Category 2 species by the U.S.D.I. Fish and Wildlife Service, until that classification code was abolished in February, 1996 (61 FR 7596, 2/28/96). The U.S.D.A. Forest Service, in Regions 2 and 4, considers this subspecies to be "sensitive", and Colorado, Utah, and Wyoming have designated it with special management status (Young 1995).

Habitat degradation, in part, has contributed to the decline of many salmonid species throughout the western United States (Williams et al. 1989; Frissell 1993). Activities that can degrade streams include improper road construction and culvert placement, dam building, mining, overgrazing, water diversion, and intensive logging. Each of these land use activities can affect any number of habitat components that are considered to be important to a biotic community. For example, food (Hawkins et al. 1983), overhead cover (Boussu 1954), instream complexity (Fausch and Northcote 1992), clean spawning gravels (Bozek and Rahel 1991), and rearing habitat (Moore and Gregory 1988a) have been positively associated with trout abundance. Habitat degradation may reduce both the quantity and quality of these attributes.

CRCT on the northslope of the Uinta Mountains have experienced a wide range of disturbance levels as a result of human activities. In the early 1900s, some drainages were used for tie-drive logging, which often scoured stream channels to bedrock. At present, these streams lack deep pools and late successional stage riparian vegetation and the beds are dominated by large, armored particles.

Habitat degradation on the northslope of the Uinta Mountains has fragmented and reduced the complexity of aquatic habitats. Habitat fragmentation is perhaps the most significant problem threatening the future survival of many species (Wilcox and Murphy 1985), and it occurs when a large area of habitat is subdivided into smaller, isolated patches (Wilcove et al. 1986). Reservoirs and irrigation diversions have eliminated migratory corridors among drainages in the Uinta Mountains. Although it is unknown how much CRCT in the Uintas may have moved within their historic range before migration barriers were created, these populations are now isolated with no opportunity for migration.

In addition to the size of a habitat, the quality of habitat is also important to a population. Complexity is one aspect of habitat quality that is thought to significantly influence the size, structure, distribution, and stability of populations. Complexity has been characterized in terms of structural components (McMahon and Hartman 1989), hydraulic variation (Lamberti et al. 1989; Pearsons et al. 1992), and a combination of depth, velocity, and substrate (Gorman and Karr 1978; Angermeier and Schlosser 1989). Complex habitats provide many important functions for stream biota. For example, the presence of complex habitats can increase a population's resistance to a

disturbance (Poff and Ward 1990; Sedell et al. 1990), and it can reduce predation risk by reducing the efficiency of a predator (Crowder and Cooper 1982). Moreover, populations in a complex habitat usually are more stable (Pearsons et al. 1992), and are more apt to recover from a disturbance (Connell and Sousa 1983), than a population living in more simple habitat. Areas with complex habitats can be considered refugia and may provide a source of colonists after a catastrophic event that results in losses in biomass or local extinctions (Sedell et al. 1990).

There is an extensive road network throughout the northslope Uintas that is used for resource extraction (e.g., logging, mining) and recreation. Poorly designed roads can affect biota by increasing sediment loadings to the stream, and improperly placed culverts can interfere with fish migration (Furniss et al. 1991). Stream reaches in the High Uintas Wilderness, however, have been less degraded than downstream reaches. The Wilderness area supports recreational use, sheep, and cattle grazing. These management activities have created a range of conditions within and among streams. The variety of habitat sizes, and varying levels of habitat complexity, provide a contrast for which to study the effects of habitat degradation.

The objective of this study was to determine how CRCT abundance and population structure were related to fragment size and several habitat features including habitat complexity. To address this objective we measured habitat variables and cutthroat trout population structure in several reaches of four fragmented headwater streams draining the north slope of the Uinta Mountains. We used these data to test several hypotheses regarding habitat use by trout and to build models

describing the use of habitat by CRCT. Our hypotheses were that adult trout densities would increase with (1) habitat complexity and (2) increasing amounts of undercut banks, large woody debris, and pools; larger substrate size, and greater residual pool depths and hydraulic retention within pools. We predicted we would observe similar patterns for juvenile trout except that juvenile trout densities would decrease with increasing residual pool depth.

STUDY AREA

We studied populations of CRCT in six streams in the Uinta Mountains, an east-west running range on the Utah-Wyoming border (Figure 1). The study streams drain north into the Green River above Flaming Gorge Dam. Many streams on the northslope of the Uinta Mountains support populations of CRCT and brook trout *Salvelinus fontinalis.* Because habitat use and growth of cutthroat trout may be affected by brook trout (Thomas 1996), we selected streams for study that appeared to contain no introduced trout. Other fish species in the study streams included mountain whitefish *Prosopium williamsoni*, mottled sculpin *Cottus bairdi*, mountain sucker *Catostomus platyrhynchus* Cope, and longnose dace *Rhinichtyhs cataractae.*

The study streams form four fragments that range in elevation from 2,590 to 3,340 m. Basin surface areas of each fragment ranged from 1.36 to 713.66 ha, and stream lengths ranged from 6.6 to 27.3 km (Table 1). The largest fragment, East Fork of Blacks Fork (EFBF), contains the East Fork and Little East Fork of Blacks Fork

River, which are third order streams (Figure 1). Meeks Cabin Reservoir is downstream of the confluence of these two streams and is a barrier to migration. Archie Creek is a tributary to the West Fork of Smiths Fork River, and these two second order streams form a fragment (WFSF). Dahlgreen Creek (DAHL), a second order stream in the Henrys Fork drainage, is fragmented from the Henrys Fork River by 2.5 km of stream channel that is dry for up to 4 months of the year thereby creating a barrier to fish migration into and out of the mainstem of Henrys Fork. Henrys Fork drains into Flaming Gorge Reservoir, thereby creating a permanent migration barrier among other fragments in the study area. Willow Creek (WILL), the smallest fragment, is a second order tributary to the West Fork of Smiths Fork River. A portion of the stream has been dewatered and trout are confined above that section.

METHODS

Habitat Data

Habitat conditions were quantified during base flows in summer 1993 and 1994. All streams were separated into reaches that were geomorphically distinct based on differences in gradient, substrate particle size, sinuosity, and valley confinement (Rosgen 1985). A 100 m section was randomly chosen for sampling in each reach. We calculated the gradient of each reach from USGS 1:24000 maps and then verified these calculations in the field with a clinometer.

We partitioned each study section into discrete habitat units of pool, riffle, or run.

We then measured the length, mean wetted width, mean depth, and the total length of undercut bank (≥10 cm deep) of each habitat unit. Maximum and tail depth of pools were also measured. Banks were categorized as stable or unstable, and the length in each category was measured (Platts et al. 1987). Stable banks were usually vegetated and characterized by a strong, well developed root system that prevented excessive erosion and sloughing. Unstable banks were poorly vegetated, showed signs of collapse, and had the potential to add excessive fine sediment to the stream.

Other factors were measured as follows. We quantified the amount of large woody debris (LWD) within the bankfull channel of the study sections by counting the number of pieces > 10 cm diameter and 3 m long within the channel. Substrate particle size distribution, water velocity, and hydraulic retention were measured in 2 randomly chosen fast units (riffles or runs) and 2 slow units (pools) in each study section. Each of the four units was divided into thirds by two transects perpendicular to stream flow. The longest axes of 20 particles were measured along each transect to the nearest one-half centimeter. Velocity and hydraulic retention were measured by introducing fluorescent dye into the top of the habitat unit. Dye was continually applied until the unit was concentrated with color. Velocity was measured as the time it took the leading edge of the dye to reach the end of the habitat unit. We defined hydraulic retention as the time it took the thalweg to clear once we stopped introducing dye into the unit.

We calculated an index of habitat complexity (HC) from the values of 5 habitat variables (percent of pool habitat, mean depth, mean particle size, percent undercut bank, and abundance of LWD). These variables were used in the complexity index

because previous studies have shown each variable to be associated with trout abundance (Faush et al, 1988) and they appeared to vary independently of one another. In developing the index, we made two assumptions: (1) the most complex habitat had "high" values for each habitat variable (i.e., 'more is better'), and (2) all variables had equal weight. We used a mathematically unbiased approach to create the index based on the Euclidean distance formula (Pielou 1984):

$$d_j = \sqrt{\sum_{i=1}^{s} (x_{ij} - x_{\max,i})^2} \quad , \qquad (1)$$

where s is the number of habitat variables, x_{ij} is the value of the *ith* habitat variable in the *jth* study section, $x_{max,i}$ is the largest defined value of the *ith* habitat variable, d_j is a measure of the distance between study section j and a hypothetical section containing maximum values of all habitat variables.

To avoid bias due to dissimilar units of measurement, each $d_{max,i}$ was scaled to range from 0 to 100%, where 100% was defined as the 95th percentile of the *ith* variable. We used the 95th percentile for each variable to avoid influential outliers. Observations exceeding the 95th percentile were converted to 100%.

The maximum possible complexity (HC_{max})is the sum of $d_{max,i}$'s, and because the value of HC_{max} is dependent upon the number of variables used, the maximum value with 5 variables is 223.61 ($\sqrt{5(100)^2}$). To scale the index so that low values represented low complexity and high values represented high complexity, HC_j, the

complexity of a given study section, was calculated as (233.61 - d_j).

Trout Survey

Prior to measuring habitat conditions in each study reach, we sampled trout with a Smith-Root® Model 7 backpack electroshocker. The upstream and downstream ends of each study section were blocked with nets to prevent fish from entering or leaving. Repeated passes were made until less than five trout were caught during a single pass. The total number of trout in a study section was estimated as the sum of fish collected in all passes. Young-of-the-year were not enumerated. After each pass, we weighed each trout to the nearest gram and measured fork length (FL) to the nearest millimeter. Other fish species were identified and counted.

Data Analysis

Trout abundance and size structure.— We assigned trout to 1 of 2 size classes after constructing a length-frequency histogram of all captured trout (n = 1967). Trout ≤125 mm FL (n = 819) were considered juveniles, and trout >125 mm FL (n = 1148) were considered adults. Adult and juvenile densities were calculated for each study reach as number / m^2.

Fragment population sizes were estimated by first calculating the overall mean densities (#/100 m^2) of adults and juveniles within a fragment from the densities of fish within each subreach and then multiplying the overall means by the total area of stream in each fragment.

Statistical analyses.— Different analyses were conducted depending on the spatial scale of observation. For reach-level data (n = 88), several regression analyses were used to determine which habitat variables were most strongly related to trout abundance and individual size, and ANCOVA was used to determine if relationships between trout abundance and habitat features varied among fragments. Although the sample size was small (n = 4), we also used regression analyses to identify any strong trends in the fragment-level data. For reach-level analyses we considered $\alpha \leq 0.05$ as significant, whereas for the fragment-level analyses, we set $\alpha = 0.10$ because of low power associated with small sample size. Juvenile and adult densities also had to be transformed ($\log_{10} x + 1$) to meet the assumption of normality required for parametric statistics. All statistical analyses were conducted with SAS® for Microsoft Windows, version 6.1 (SAS 1993).

Regression analyses. Three sets of regression analyses were conducted at the reach spatial scale. In the first set of analyses, we regressed trout densities and individual size against the complexity index (CI). We then regressed trout densities and size against the 6 different habitat variables that we predicted should influence trout abundance (% pool habitat, residual pool depth, mean particle size, % undercut bank, LWD abundance, and hydraulic retention), 5 of which were used to construct CI. After conducting these analyses, we then ran a series of step-wise regressions with the original 6 habitat variables plus 4 others (i.e., channel gradient, elevation, mean channel width, and mean channel depth) to identify other potentially important variables.

RESULTS

Variation among reaches

Most of the habitat and trout variables showed considerable variation among the study reaches (Table 2). Of the habitat variables, the amount of undercut banks, hydraulic retention, and amount of LWD were most variable (see CVs). Elevation, mean channel depth, residual pool depth, and habitat complexity appeared least variable. Densities of both adult and juvenile trout were generally more variable among reaches than were habitat features, although individual sizes of the two life stages were considerably less variable than densities.

Reach-level analyses

Tests of hypotheses.— The habitat complexity index was not related to juvenile trout density, and was only weakly related to adult density (r^2 = 0.035). However, some of the variables used to construct HC were independently related to trout density.

Three of the 6 habitat variables predicted to be related to trout abundance were significantly related to adult trout density (substrate size, residual pool depth, and hydraulic retention), however both residual pool depth and hydraulic retention time were negatively related to adult trout density, opposite the expected relationship (Table 3). Adult trout density was positively related only to mean substrate size. Our initial model was slightly more successful in predicting densities of juvenile trout. Densities increased with amount of LWD and decreased with residual pool depths as expected.

Densities were unrelated to the other habitat variables.

Stepwise regressions.— The stepwise regressions suggested that relatively few habitat features were related to trout densities and size (Table 4). Adult trout densities increased strongly as elevation of the reach increased(Fig. 2) and declined with increasing hydraulic retention time. This stepwise regression accounted for 57% of the variation in adult densities. The stepwise regression on juvenile densities identified only one significant variable (mean channel depth). Juvenile densities declined with increasing channel depth, but the model accounted for only 10% of the variation in densities.

Adult size was strongly related to both elevation and channel width, and this model accounted for 61% of the variation in adult size. Juvenile size was related only to hydraulic retention and declined as retention increased. The model accounted for only 9% of the variation in juvenile size.

Fragment-specific responses.— ANCOVA revealed that the slopes defining the relationships between trout density and habitat factors seldom varied among fragments (Table 5). Only 1 significant fragment×habitat factor interaction occurred among the 12 examined (6 habitat factors × 2 size classes). The only significant interaction occurred for adult trout and was between undercut banks and fragment. This analysis showed that adult trout densities increased with increasing amounts of undercut banks, but that the degree of increase to the same change in amount of undercut bank varied among fragments. No interactions occurred for juvenile trout.

We observed several cases where the slope of a relationship was similar among

fragments, but densities varied among fragments for a given amount of a habitat variable. For example, adult trout densities varied significantly among fragments while increasing with percent of the channel as pool and decreasing with the amount of LWD in a similar way within all fragments. Similarly, juvenile trout densities increased with substrate size in a similar fashion within all fragments. These results suggest that while the fundamental relations between trout and some habitat factors were similar among fragments, some other features associated with fragment were influencing trout densities.

Separate regression analyses by fragment indicated that adult density was not related to undercut bank in either EFBF or DAHL, but it was significantly related to undercut bank in WFSF (r^2 = 0.29) and WILL (r^2 = 0.44). Additionally, WILL was the only fragment that showed a significant relation (+) between adult density and residual pool depth (r^2 = 0.54).

Fragment-level analyses

Fragment size was positively related to cutthroat trout population size (r^2 = 0.89), adult trout abundance (r^2 = 0.91), and adult density (r^2 = 0.84), but was not related to juvenile abundance or juvenile density. Mean habitat complexity among fragments was positively related to adult density (r^2 = 0.84), but was not related to population sizes or juvenile density. The proportion of adults in the population increased significantly as fragment size increased (r^2 = 0.99, Fig. 3) as did the mean length and weight of adult trout (r^2 = 0.92 and 0.90, respectively). The mean length and mass of juvenile trout

were not significantly related to fragment size.

DISCUSSION

Importance of habitat complexity

Contrary to expectation, our measure of habitat complexity was not consistently related to trout abundance. Moreover, in the 1 case where there was a strong relationship between CI and adult trout density, CI and fragment size were confounded and the relationship between trout density and CI could have been spurious. At least three interpretations of these data are possible. First, habitat complexity may not be as important to CRCT as theory and previous observations for other species would suggest. We have no basis for evaluating this possibility. Second, populations may not have been at or near carrying capacity and thus we would not expect to observe strong relationships between trout abundance and any habitat factor, including an aggregate factor like complexity. Differences among reaches in angling and natural mortality could conceivably create populations that differed considerably in how close to carrying capacity they were. If so, local populations would have differed in the degree to which they were limited by available habitat and few cross-reach patterns would have emerged. At this time, we have no information about the carrying capacity of individual reaches. A third possibility is that trout may perceive complexity differently than we did. Complexity may in fact be important to trout, but we simply failed to adequately measure it. This interpretation has merit, because some of the individual

factors used to construct the complexity index were related to trout abundance. Moreover, the direction of these independent relationships were not always similar, i.e., trout increased with increasing values of some factors but decreased with others. These opposing tendencies may have been partially responsible for the general lack of a relationship between trout and CI since the independent responses would tend to cancel one another.

Lack of responses to complexity has been observed elsewhere. Schlosser (1995) also found that complexity was not important at the small scale. In a Minnesota stream, he discovered that <5% of the variation in fish abundance, in pools and riffles, was associated with habitat complexity. He reported that seasonal and annual environmental variation were more important in influencing fish abundance. Other factors, such as food (Wilzbach 1985), for instance, also may be more important to fish at a small scale.

Fish habitat relations and potential limiting factors

Our initial hypotheses about which habitat factors would be related to trout abundance and size were generally not supported by our data. It may have been unrealistic to expect to observe significant, and predicted, relationships for all 6 variables considering that such a response would imply simultaneous limitation by several variables. If we assume one factor would be most limiting, the availability of large particle sizes would appear to be the most important factor for adult CRCT. In contrast, the availability of larger amounts of LWD and shallower pool depths appear to

be most important to juveniles.

Habitat requirements differ for juvenile and adult salmonids (Cunjak and Power 1986; Moore and Gregory 1988b; Bozek and Rahel 1991; Fausch and Northcote 1992; Nickelson et al. 1992). In this study, adult trout were most abundant in sections that had large substrates and a high percentage of undercut banks. Undercut banks are perhaps the most important cover type in streams (Behnke and Zarn 1976), and increases in cover can yield an increase in trout abundance (Boussu 1954; McMahon and Hartman 1989). Heggenes et al. (1991) reported that coastal cutthroat trout in Musqueam Creek used overhead cover more frequently than instream cover, and undercut banks were the preferred overhead cover type. We suspect that larger substrates also provide cover for trout either from summertime predators or as refugia during winter.

The observed relationships for juvenile trout are consistent with many previous observations. Young trout were most abundant in subreaches that had abundant large woody debris and shallow pools. LWD offers hiding cover and reduced currents for small fish, and as pool depth gets larger small fish may be at either a competitive disadvantage with bigger fish or be at risk of predation by these same fish and other piscivorous animals. Others have also found juvenile fish associated with LWD (Moore and Gregory 1988b; McMahon and Hartman 1989; Black 1996). Woody debris appears to be important to young fish as it dissipates stream energy (McMahon and Hartman 1989) and can channel water toward the banks creating lateral habitats needed by juvenile salmonids (Carlson et al. 1990; Bozek and Rahel 1991). Fausch

and Northcote (1992) found biomass of juvenile salmonids highest in sections of Musqueam and Cutthroat Creeks where a high number of pieces of LWD influenced the channel.

In EFBF, where LWD was least abundant, most trees spanned the channel upon falling. Had the logs landed in the channel, they probably would have been "effective" in creating juvenile habitat (Fausch and Northcote 1992). The absence of large wood was not the only habitat component that juveniles in EFBF lacked. Juvenile trout typically occupy positions in slower and shallower water than adults (Cunjak and Power 1986) and EFBF had the highest mean depth and velocity, suggesting that juvenile habitat could be limiting.

Elevational gradients

The ANCOVA results implied that trout generally responded to a habitat feature in much the same way regardless of stream, but that the different fragments had different capacities to produce trout. The stepwise regression analyses revealed a very strong dependence of adult CRCT densities and individual size on elevation. There are several possible reasons that adult trout would be sensitive to elevation. First, angling could have removed large fish from more accessible, lower-elevation reaches. Second, habitat conditions could be better at higher elevations. This latter interpretation is consistent with the way those habitat variables related to adult trout density vary with elevation. Elevation was negatively related to hydraulic retention and LWD and positively related to substrate size and amount of undercut banks. Although

it is impossible to determine from these data the actual causes for the observed elevational gradient in adult trout densities, it is likely that several factors are acting in concert to create this pattern.

CONCLUSIONS

Both fragment size and habitat quality appear to be important to cutthroat trout. However, the combination of habitat quality and fragment size may be more important to a population than either factor considered alone (Boecklen 1986; Angermeier and Schlosser 1989). A population living in a habitat with low habitat quality probably requires more area than the same sized population living in a highly complex fragment. A large range of fragment sizes with varying levels of habitat quality are needed to rigorously test this hypothesis. Unfortunately, there are not enough allopatric populations of cutthroat trout on the northslope to test if, or to what extent, habitat quality compensates for fragment size. An understanding of this relation will become increasingly more important as habitats continue to be fragmented and reduced in size.

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Table 1. Physical characteristics of the 4 fragmented stream systems: Willow (WILL), Dahlgreen (DAHL), West Fork of Smiths Fork (WFSF), and East Fork of Blacks Fork (EFBF). Units for LWD (pc) = pieces per 100 m of channel. CI = complexity index.

Fragment	n	Area (m^2)	Length (m)	Mean Width (m)	Mean depth (m)	Residual depth (m)	Undercut bank (%)	Pool habitat (%)	Pebble size (cm)	Dye retention (s/m)	LWD (pc)	CI
WILL	10	13570	7422	1.83	0.10	0.18	4.68	21.23	10.81	42.28	11.50	78.81
DAHL	7	14276	6555	2.18	0.14	0.21	8.04	26.43	12.62	58.00	5.00	85.19
WFSF	41	91111	26333	3.46	0.18	0.30	10.31	21.94	13.47	28.06	3.56	81.89
EFBF	30	136558	27331	5.01	0.21	0.26	15.33	30.98	17.41	8.22	2.97	103.26

Table 2. Mean, minimum, and maximum values and coefficients of variation (CV × 100) for the environmental and trout variables used in the analyses. In some cases, n ≠ 88 because of missing data.

Variable and units	n	Mean	Minimum	Maximum	CV
Environmental Variables:					
Elevation (m)	88	2920	2591	2920	6
Gradient (%)	88	4.0	0.0	15.0	72
Width (m)	88	3.7	1.1	8.3	47
Depth (m)	88	0.18	0.07	0.49	35
Residual depth (m)	83	0.27	0.12	0.54	34
Undercut bank (%)	88	11.2	0.0	71.5	107
Pool habitat (%)	88	25.3	3.2	75.6	50
Substrate size (cm)	88	14.4	0.1	30.5	39
Retention (s/m)	76	24.9	3.7	137.0	103
LWD (pc/100m)	88	4.4	0.0	23.0	129
Habitat complexity	88	89.1	24.7	161.9	27
Trout Variables:					
Adult trout density (#/100 m^2)	88	3.3	0.0	17.7	115
Juvenile trout density (#/100 m^2)	88	1.7	0.0	32.9	166
Adult trout length (mm)	81	172	128	217	11
Juvenile trout length (mm)	78	96	54	120	14
Adult trout mass (g)	78	57.8	20.2	96.9	33
Juvenile trout mass (g)	76	10.9	0.3	20.0	36

Table 3. Results of the regression analyses testing if 6 habitat features were related to trout abundance. RC = regression coefficient. The last column describes agreement with initial predictions: SA = strongly agree (statistically significant in predicted direction, WA = weakly agree (not significant but right direction), D = disagree (either no relationship or in opposite direction as predicted).

Dependent Variable	Independent Variable	RC	P	Prediction ?
Adult Density	Intercept	0.405	0.035	
	Undercut Banks	0.009	0.065	WA
	Substrate Size	0.019	0.009	SA
	Residual Pool Depth	-0.933	0.035	D
	Hydraulic Retention	-0.004	0.012	D
	LWD	-0.011	0.051	D
	% Pool	0.004	0.214	WA
Juvenile Density	Intercept	0.667	0.006	
	Undercut Banks	-0.005	0.398	D
	Substrate Size	-0.000	0.979	D
	Residual Pool Depth	-1.124	0.042	SA
	Hydraulic Retention	0.000	0.778	D
	LWD	0.015	0.044	SA
	% Pool	0.003	0.440	WA

Table 4. Results of the stepwise regression analyses of trout density (log (x+1) / $100m^2$) and individual size (g) on 11 habitat features. RC = regression coefficient.

Dependent Variable	Independent Variable	RC	P	Model R^2
Adult Density	Intercept	-2.878	0.000	0.57
	Elevation (km)	1.182	0.000	
	Hydraulic Retention	-0.003	0.006	
Juvenile Density	Intercept	7.717	0.000	0.10
	Mean Channel Depth	-25.944	0.003	
Adult Size	Intercept	-460.714	0.000	0.61
	Elevation (km)	252.190	0.000	
	Channel Width	16.744	0.000	
Juvenile Size	Intercept	318.369	0.000	0.09
	Hydraulic Retention	-212.155	0.009	

Table 5. Results of the analyses of covariance testing if relationships between trout abundance and habitat features varied among stream fragments. If the interaction term was not significant, the analysis was run again without the interaction term in the model. Results of the final models are shown.

Variable	Source	F	P
Adult Density	Undercut Banks	5.19	0.025
	Fragment	12.47	0.000
	Interaction	3.50	0.019
	% Pool	4.81	0.031
	Fragment	12.09	0.000
	Hydraulic Retention	0.73	0.397
	Fragment	7.65	0.000
	LWD	7.76	0.007
	Fragment	14.45	0.000
	Substrate Size	0.00	0.960
	Fragment	13.15	0.000
	Residual Depth	0.06	0.804
	Fragment	18.03	0.000

Table 5 (continued).

Variable	Source	F	P
Juvenile Density	Undercut Bank	0.12	0.726
	Fragment	16.49	0.000
	% Pool	0.22	0.639
	Fragment	16.58	0.000
	Hydraulic Retention	3.32	0.073
	Fragment	15.22	0.000
	LWD	0.94	0.334
	Fragment	11.77	0.000
	Substrate Size	5.15	0.026
	Fragment	19.68	0.000
	Residual Depth	1.34	0.250
	Fragment	12.18	0.001

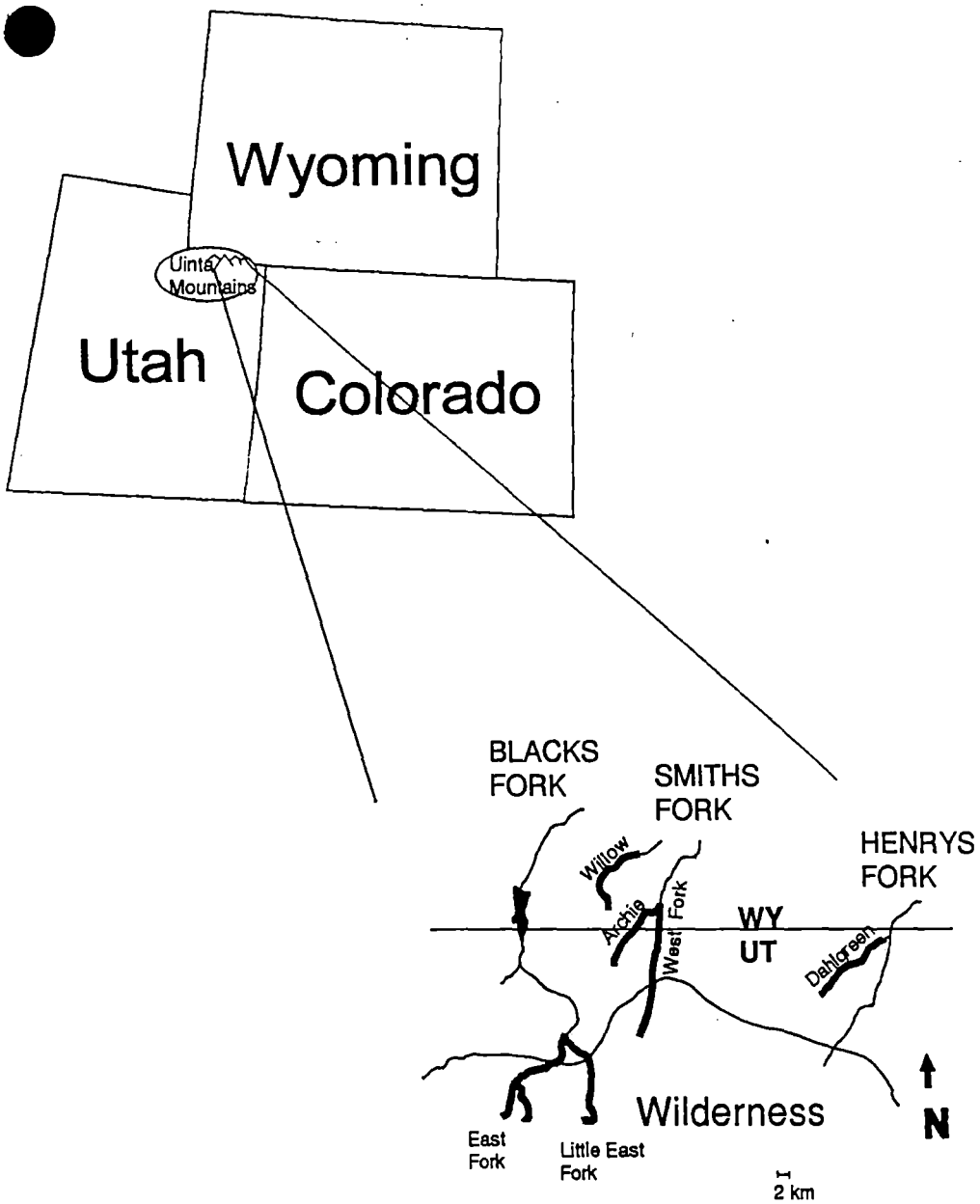

Fig. 1. Study area in the Uinta Mountains. Six streams form four fragments: (Willow), (2) Dahlgreen, (3) West Fork of the Smiths Fork, which includes Archie Creek, and (4) East Fork of the Blacks Fork, which includes Little East Fork of Blacks Fork.

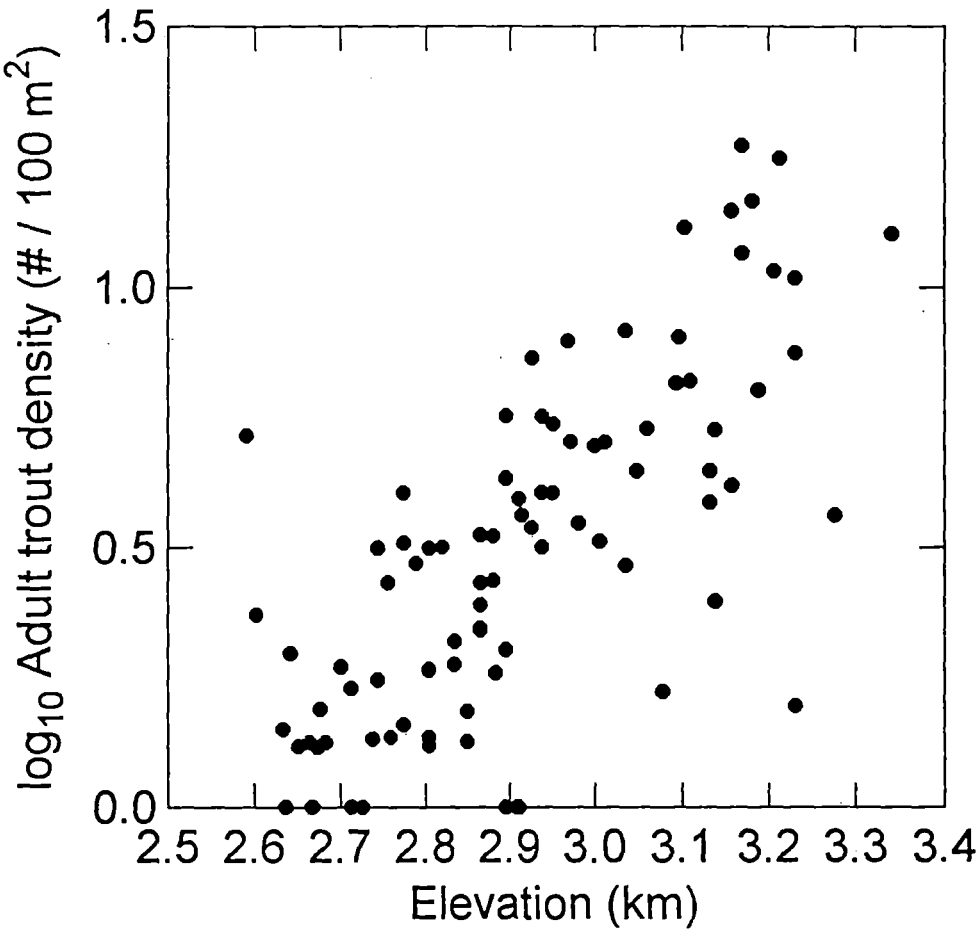

Fig. 2. Relationship between adult density and elevation.

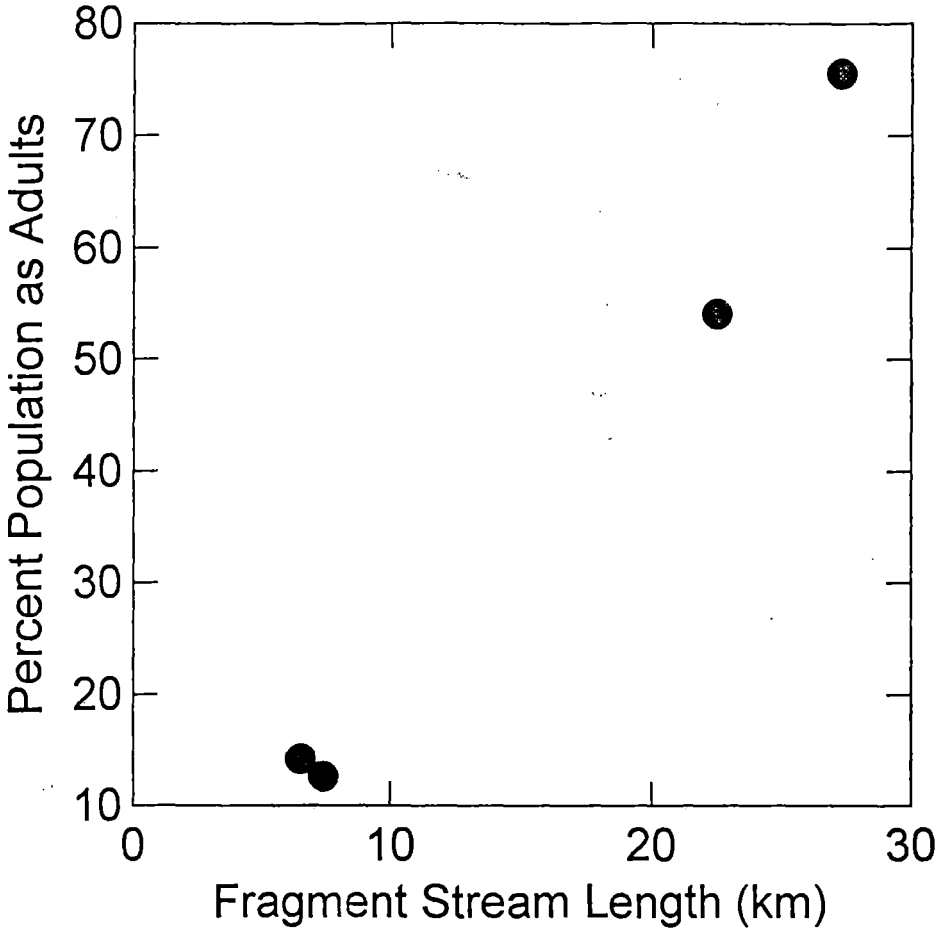

Fig. 3 Relationship between percent of the population as adults and fragment size.

CHAPTER II

Assessing Population Attributes and Habitat Requirements of a size-structured Colorado River Cutthroat Population in Fragmented Watersheds: A Case Study

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Abstract

Fragmentation has reduced the historic range of Colorado River cutthroat trout *Oncorhynchus clarki pleuriticus* and presumably increased this subspecies' risk of extinction. This paper addresses alternative approaches to analyzing stage structured populations at the reach, tributary and basin spatial scales. We address how densities and size structure of Colorado River cutthroat trout are associated with differences in habitat richness and diversity for different size classes.

We sampled 88 - 100 m reaches in 4 fragmented stream basins in the Uinta Mountains of northeast Utah that differed in size. In each basin we quantified habitat conditions (basin area and stream length; channel depth, width, and residual pool depth; amount of undercut banks, pool habitat, and large woody debris; substrate size; and hydraulic retention time) and densities of juvenile and adult cutthroat trout.

Discriminant functions analyses was used to generate models based on habitat variables to describe and predict where 4 size class of cutthroat trout were present or absent. Models successfully predicted distributions in 70% of all cases. Habitat richness and diversity indices were then calculated using the discriminant functions at the within reach, within tributary and among basin scales. The subbasin with the highest trout density and highest size class diversity also had the highest habitat at all spatial scales. While the subbasins with the largest area had the highest number of quality habitat units, they did not have the highest diversity of usable habitats for the various size classes of trout suggesting that bottlenecks probably exist within the life cycle of the fish.

INTRODUCTION

Native inland salmonids are increasingly at risk due to loss of habitat area and complexity. Habitat fragmentation is perhaps the most significant problem threatening the future survival of many species (Wilcox and Murphy 1985). Fragmentation is particularly harmful to small, segregated populations that live in relatively small fragments. As the degree of isolation increases, populations may face an increased risk of local extinction due to demographic and environmental sn due to demographic and envirc 1981, Shaffer and Samson 1985). Natural disturbances, such as fire, drought, and flooding all pose a threat to small populations, and superimposing anthropogenic disturbance over natural disturbance regimes may in some cases accelerate extinction (Reeves et al. 1995). Large fragments generally will favor population persistence (Wilcove et al. 1986), as a large area can buffer against catastrophe, contains a higher diversity of habitat types (MacArthur and Wilson 1967), and typically can support more resources, individuals, and species than smaller fragments (Connor and McCoy 1979; Angermeier and Schlosser 1989).

In addition to size, the quality of habitat in a fragment may be important to a population. The presence of complex habitats is thought to influence the size, structure, distribution, and stability of populations and may increase a population's resistance to a disturbance (Poff and Ward 1990; Sedell et al. 1990). Moreover, populations in a complex habitat usually are more stable (Pearsons et al. 1992), and are more apt to recover from a disturbance (Connell and Sousa 1983), than a

opulation living in more simple habitat. Areas with complex habitats may act as efugia and provide a source of colonists after a catastrophic event that results in evere population declines or local extinctions (Sedell et al. 1990).

At all scales, the quantification of stream habitat attributes is important in escribing the quality and the quantity of habitats available to different life stages. Stream structural components form a complex of mosaic of habitats that are important o salmonid survivorship and reproduction. For instance, undercut banks, large woody ebris, and substrata are habitat components that can provide cover for young and dult fish. Structure increases the complexity of a channel when it alters channel epth, produces hydraulic diversity, creates refugia at high flows, and provides verhead cover at low flows. Instream wood may affect channel morphology, and in ome streams it is the dominant pool forming structure (Andrus et al. 1988; Fausch and Northcote 1992). Complexity has been characterized in terms of structural components McMahon and Hartman 1989), hydraulic variation (Lamberti et al. 1989; Pearsons et al. 1992), and a combination of depth, velocity, and substrate (Gorman and Karr 1978; Angermeier and Schlosser 1989). The underlying assumption is that highly complex habitats produce high fish densities. However, density or biomass is not always evidence of high-quality habitat (Van Horne 1983): Low-quality habitats, or sinks, may support large populations when high-quality habitats produce a surplus of individuals (Pulliam 1988).

Assessing the quality, quantity, and the juxtaposition of habitats is an important step in any conservation program. In addition, establishing the relationship between

knowledge of habitat characteristics and their importance to population structure and size gives managers important information on which habitat characteristics may be most important, the scale at which these characteristics are important, and may help to determine where restoration may be most effective.

Until recently, there have been few attempts to determine the degree of fragmentation and the quality of habitat fragments over large landscapes. At the basin scale attempts have been made to assess habitat quantity and quality with mixed success (Thomas et al. 1993, Thomas and Dombeck 1994). Typically, small suites of variables that have perceived importance to salmonid life histories have been measured and their values compared to "reference" conditions to establish watershed quality ratings. These attempts were limited by data consistency, quantity, and quality, and used a limited number of variables that may not have captured the full range of habitat characteristics that may have relevance to fish. No attempts were made to develop comparative or predictive models.

At smaller scales, researchers have attempted to develop predictive models that relate habitat variables to fish populations, but these generally have not been used to assess broad-scale habitat conditions and conservation potential. Lanka et al. (1987) related watershed-level variables with fish densities to predict which variables may be important in explaining fish abundance. They were able to explain a higher proportion of the total variation in trout densities using large-scale variables than smaller scale (channel unit) variables. Binns and Eiserman (1979) used a combination of larger scale variables (late summer streamflow, annual streamflow variation) and smaller-

scale variables (e.g. cover, bank condition, stream width) to assess the productive potential of fluvial habitats in Wyoming. They developed predictive models relating the abundance of trout to habitat quality.

Generally, habitat relationships studies have related standing crop or total density estimates to habitat variables (Fausch et al. 1988). Limitations of these models include low predictive power, limited applicability to specific regional areas, and lack of relevance to specific life stages within the population. We believe this last shortcoming may be most important for questions concerning species viability and conservation potential, and that habitat models must address the habitat needs of all life stages of the population. The objectives of this study were to (1) describe the specific habitat attributes that were important to Colorado River cutthroat trout in streams (CRCT), (2) describe differences in habitat attributes by stage structure, (3) describe watershed-level differences in habitat potential for conserving CRCT using the above information.

STUDY AREA

The data for this study were collected from streams draining the Uinta Mountains, an east-west running range on the Utah-Wyoming border. The study streams drain north into the Green River above Flaming Gorge Dam. To minimize biotic interactions thereby simplifying analysis interpretation, only streams without brook trout, a known competitor with cutthroat trout (Thomas 1996) were sampled in this study. Other native fish species present included mountain whitefish *(Prosopium williamsoni)*, mottled

sculpin (*Cottus bairdi)*, mountain sucker (*Catostomus platyrhynchus* Cope), and longnose dace (*Rhinichtyhs cataractae)*.

The study streams were selected from four fragmented subbasins that range in elevation from 2,590 to 3,340 m. Subbasin surface areas range from 13, 582 to 136,393 m^2 and in total stream length from 6,555 to 27,331 m. The largest subbasin, East Fork of Blacks Fork (EFBF), contains the East Fork and Little East Fork of Blacks Fork River, which are third order streams. Archie Creek is a second order tributary to the West Fork of Smiths Fork River (also second order). These streams comprise the West Fork (WFSF) subbasin which is isolated from the remaining basin by water diversion structures. Dahlgreen Creek (DAHL), a second order stream in the Henrys Fork drainage, is isolated by a 2.5 km of the stream which has only subsurface flow near the confluence with Henrys Fork River. Henrys Fork drains into Flaming Gorge Reservoir, thereby creating a permanent migration barrier. Willow Creek (WILL), the smallest isolated subbasin, is a second order tributary to the West Fork of Smiths Fork River. A portion of the creek has been dewatered confining trout above that section.

METHODS

Physical Habitat Data

All streams were surveyed at base flows in summer 1993 and 1994. Streams were visually separated into reaches that were geomorphically distinct based on changes in gradient, substrate particle size, sinuosity and valley confinement (Rosgen 1985). A 100 m subreach was randomly chosen from each reach as a representative

subsample of the reach. The gradient of each reach was estimated from USGS 1:24000 maps and then verified my calculation in the field with a clinometer.

Each subreach was categorized into discrete habitat units of pools or riffles. In each unit we measured the habitat length, mean wetted width, mean depth, and the total length of undercut bank, if the undercut was ≥10 cm deep. Maximum depth and tail depth were also recorded. Banks were categorized as stable or unstable and the length in each category was measured (Platts et al. 1987). Stable banks were usually vegetated and characterized by a strong, well developed root system that prevented excessive erosion and sloughing. Unstable banks were not well vegetated, showed signs of collapse, and had the potential to add excessive fine particles to the stream.

Instream large woody debris (LWD) was categorized as (1) single pieces (>10 cm diameter and 3 m long), (2) aggregates (≥2 single pieces in contact with one another and trapping debris), or (3) rootwads (Overton et al. 1993). Only wood found within the bankfull channel was enumerated. The length, diameter, and percent submergence was measured for each category. In addition, the volume of each wood aggregate and root wad was measured, as well as the number of pieces of wood in each aggregate.

At least two pools and two riffles were randomly chosen from each subreach to measure particle size distribution, velocity, and hydraulic retention. Each of the randomly selected units was divided into thirds by two transects from which twenty particles were randomly selected. We measured the longest axis of each particle to the nearest one-half centimeter. Velocity and hydraulic retention were measured by introducing fluorescent dye into the top of the habitat unit. Dye was continually applied

unit was uniformly concentrated with color. Velocity was measured as the time it took the dye to reach the bottom of the habitat unit. We defined hydraulic retention as the time it took for the thalweg to be clear of dye at the bottom of the unit.

Cutthroat Trout Sampling

To estimate trout population sizes, densities and size structure, we sampled cutthroat trout in subreaches of approximately 100 m immediately before habitat sampling. The upstream and downstream ends of each subreach were blocked with nets to prevent fish from entering or leaving. Fish were collected with a Smith-Root Model 7 backpack electroshocker. We continued sampling a section until less than five trout were caught on the final pass. After each pass, each trout was weighed to the nearest gram and the total length to the nearest millimeter. Other fish species were identified and counted.

Data Analysis

Cutthroat trout were divided into four size groupings based on the length-frequency histogram of all captured trout (n = 1967). We classified the two smallest size classes as "juvenile fish" and were < 80 mm FL and 81-125 mm FL, respectively (n = 819). A subadult size class (126-160 mm FL) and adult class (>160 mm FL) were also noted. A total of 1148 fish comprised these two larger size classes. Densities of these size classes were estimated for each reach by dividing the total number fish by the average area of the sampled subreach. Densities were $\log_{10}$-transformed (value + 1) to

normalize the data and to stabilize the variance structure.

To determine which habitat variables explained and predicted the presence of each size class of cutthroat trout, each sample point was characterized by the presence or absence of each particular size class of fish. These presence/absence codes were then used in a discriminant functions analysis, with all of the physical habitat variables and the densities of other fish species as the continuous, independent variables. All independent variables were tested for normality and transformed in needed, prior to the final analysis. A separate analysis for each size class of cutthroat trout was performed.

Multiple regression equations were derived from the discriminant functions analysis which provided predictions regarding whether the complex of habitat variables at each site were sufficient to predict the presence of each size class of trout. Habitat variables from each site were used in these equations to categorize each site with respect to habitat suitability for each of the four size classes. This allowed us to identify subreaches that had high quality habitat for one or more of our size classes of trout, but from which we failed to find fish.

Using the predicted presence/absence categories for each size class of fish, we then calculated the richness and Simpson's Diversity (Begon et al. 1990) of habitat types found in each sampled reach. Richness values range from 0 for sites with no predicted habitat for any fish size class to 4 for sites with all habitat types available. Richness and diversity values, as well as fish densities for each size class and total fish densities were then compared among the four isolated subbasins using one-way analysis-of-variance. Post-hoc multiple comparisons were performed using the Ryan-

E[redacted]-Gabriel-Welsch algorithm (Day and Quinn 1989). Finally, regression analyses regressing the various fish indices against habitat richness and diversity indices were performed. Regressions were run at three spatial scales; using each subreach as a statistical unit (n=88), using the means from streams as independent units (n=6) and finally using the overall values for each subbasin (n=4). The hypothesis being tested with these analyses is that the overall cutthroat trout population size estimated for each subbasin is best explained by the diversity of size-specific habitats available. This hypothesis differs from most analyses found in the literature which attempt to explain total fish diversity, averaged across all life-history stages, using a combination of habitat variables.

All statistical analyses were performed using SAS for Microsoft Windows, version 6.1 (SAS 1993). We set *a priori* significance levels to $\alpha = 0.10$ because of perceived low power due to limited sample sizes.

RESULTS

Discriminant functions analyses resulted in significant predictions for the presence/absence of each size class of cutthroat trout using varying combinations of habitat variables. For the smallest size class, fish presence was negatively associated with the amount of wood aggregates in the bank-full channel and the amount of submersed wood and positively associated with the coefficient of variation for stream width (Table 1). This model described 20% of the variation, correctly classifying 47 of

the 87 sampled units. Thirty of the erroneous classifications were due to sections that were predicted to have suitable habitat but yielded no small fish. For the second size class (81-125 mm FL), fish presence was positively associated with the coefficient of variation for substrate size and the coefficient of variation for velocity and negatively associated with the presence of dace, the amount of stable banks, the number of riffles within the sampled area, elevation, mean substrate size and the coefficient of variation for residual pool depths (Table 2). This model explained 68% of the variation and correctly classified 57 of the 71 sites. As with the first model, 67% of the misclassified sites were due to areas predicted to have fish where there were no fish present. For the third size class (126-160 mm FL), fish presence was positively associated with mean substrate size and the coefficient of variation for hydraulic retention, and negatively associated with the size of coarse woody debris, dace densities, the amount of root wads, the coefficient of variation for stream width and the amount of stable banks (Table 3). The overall model explained 64% of the variation with 64 of the 76 sites being correctly classified. An equal number of misclassifications was observed for both predicted fish presence and absence. For the largest size class of fish (>160 mm FL), fish presence was positively associated with the coefficient of variation of maximum pool depth and the amount of coarse woody debris dams and negatively associated with retention time, the amount of root wads and the coefficient of variation for substrate size (Table 4). This model explained 41% of the total variation with 55 of 64 sites being correctly classified. All mis-classifications occurred because some sites were predicted to have large fish with no fish being found.

Analyses of variance, comparing fish size classes, overall densities among the four watersheds revealed that significant differences occurred among the subbasin fragments. The smallest size class showed highly significant different densities among subbasins ($F=11.96$, $p<0.0001$, $df=3,84$) with the highest density found in the WILL basin followed by DAHL. The WFSF and EFBF densities of small fish were not different from each other but were different from the other two areas. The larger juvenile size class showed a very similar pattern ($F=20.33$, $p<0.0001$, $df=3,84$) with the exception that the DAHL, WFSF and EFBF densities were not different from each other but were significantly less than that found in the WILL subbasin. The small adult size class showed no significant pattern among subbasins ($F=2.26$, $p=0.0875$, $df=3,84$). The largest size class was most dense in the EFBF and WILL subbasins and least dense in the DAHL and WFSF subbasins ($F=14.65$, $p<0.0001$, $df=3,84$). When taken in aggregate, the total density of cutthroat trout was different among subbasins ($F=10.57$, $p<0.0001$, $df=3,84$) with the highest overall density found in the Willow subbasin. Densities in all other subbasins were not significantly different from each other.

Richness indices calculated within each reach for size-specific habitats based on the discriminant functions models revealed significant differences in habitat among subbasins. The average reach-level habitat richness of predicted habitats was highest in the WILL and EFBF subbasins and lowest in the DAHL and WFSF subbasins ($F=6.40$, $p=0.0006$, $df=3,84$).

Finally, regressing the diversity of size classes of fish against the diversity of

predicted habitats at the reach, stream and subbasin scale resulted in increasing explanatory power with increasing scale. No significant dependence was observed between size class diversity and habitat diversity using each reach as a replicate ($F=0.010$, $p=0.9245$, $df=1,86$, $R^2=0.0025$). The same regression using total values from each stream was not significant, but explained more variation that at the reach scale ($F=1.318$, $p=0.2542$, $df=1,5$, $R^2=0.20$). Using diversity values for whole subbasins yielded a significant positive relationship ($F=14.160$, $p=0.0356$, $df=1,3$) that explained 45.12% of the variation in fish size-class diversity.

DISCUSSION

Understanding the limiting factors associated with populations of plants and organisms is of central importance to both basic ecology and conservation biology and management. In many cases, habitat degradation due to human exploitation and activity is known or suspected to result in habitat limitation. This has been especially true in stream and riverine systems where loss of riparian habitat and fragmentation of watersheds due to water diversions and dams have resulted in large scale depletions of habitable areas. Numerous studies exist in which physical and biotic data have been collected and used to determine and predict those variables most likely to influence fish abundances and distributions (Fausch et al.1988, Lanka and Hubert 1987, Binns and Eiserman 1979). The most common approach is to collect fish and habitat variables in localized areas such as habitat units (sensu Hawkins et al. 1983) or reaches (Lanka et

al. 1987) and then use multiple regression analyses to determine habitat associations (see review by Fausch). While this approach can and often does provide valuable insight into the small scale habitat variables associated with fish densities, it is unclear how well it predicts the long term stability or habitat requirements of the overall fish population. This approach is especially problematic for rare or declining species since the regression approach requires that good habitats be used by high numbers of individuals in order for the habitat-density relationship to be quantified. Because declining or small populations may not be using all available habitats at a particular local scale, these models often result in extremely low predictive power.

A second potential problem with the above mentioned statistical approach to quantifying habitat-density relationships lies in the estimation of the density. In most cases, all size (or age) classes of individuals are pooled together to derive the population density (or standing crop). The habitat association model produced by regression can only be interpreted as the habitat requirements for all life-history stages of the organism in aggregate. Because many organisms, including fish, exhibit very marked ontogenetic changes in their behavior and ecology, the overall models become very diffuse.

Finally, because the biological and physical habitat data are typically collected at small scales (< 300m), the derived physical habitat association models must be extrapolated in order to make any predictions at the population level. This becomes especially problematic when different stage classes of organisms use different habitats on a seasonal basis.

In an attempt to utilize data collected at small scales for population-level inquiries, we used an alternative approach to data analysis and interpretation in this study. Rather than treat size classes of fish as continuous density estimates, we simply categorized each sampling unit as having that size class of fish present or not. Discriminant functions analyses allowed us to utilize the small-scale habitat variables to identify those sites that possessed the necessary habitat characteristics for each size class of fish. The models generated correctly predicted the utilization of all fish size classes 78% of the time. of the 75 misclassified sites, 72% were predicted to have fish where no fish were observed. We believe this to be common of many data sets, especially those dealing with rare or declining populations and illustrates how continuous habitat association models may provide inaccurate assessments.

Rather than pooling all fish and then comparing overall densities or standing crops among statistical units, we analyze each size-class (derived from length-frequency histogram) separately and then in combination. This allows for the stage structured integrity, know to be important in fishes (Werner and Gilliam 1984, Schlosser 1991, Schlosser and Angermeier 1995), intact. The results of these comparisons show that the Willow subbasin has the highest density of juvenile (both size groups) and large adults. The EFBF subbasin had an equally high density of adults, but very few fish from any other size class. These patterns are not predictable nor explainable based on multiple regression analyses alone (Horan 1996).

Using the habitat discrimination functions derived, we calculated the richness of habitats predicted to exist at each reach. Because these computations were performed

each site sampled, the highest possible richness value for habitats is 4; one for each size class of fish. Because of the finite maximum, richness and diversity values are identical at this scale. Analysis of variance results yielded our expected result in that the highest habitat richness was found in the Willow Subbasin. A slightly lesser amount of predicted habitat was observed in the EFBF subbasin. The WFSF and DAHL subbasins had significantly less habitat richness than the other two subbasins.

Because population viability and stability require recruitment to the adult life stage, stable populations must at some times have individuals at all life stages. When this is the case, the diversity of size classes or life stages should be high. Because the discriminant functions analyses resulted in different habitat variables being important for each life stage, we suggest that there may be a relationship between the diversity of habitats and the diversity of fish size classes. Ultimately, these criteria may provide us with the greatest insight into which populations have the greatest propensity of persistence. Furthermore, we envision spatially dependent associations between these derived measures. Localized population diversity should be driven by localized habitat variation while basin-wide populations should reflect much larger scale habitat variation (such as differences among tributaries and upstream/downstream river sections). Regression analyses at different spatial scales (within reaches, within streams, within subbasins) suggest that localized population size class diversity is unaffected by localized habitat variation. This finding is not surprising, since most standard approaches to small scale habitat associations result in good fits between fish densities and continuous habitat measures (see papers in Matthews and Heins 1987). As the

scale of analyses increased, the association between size structure and habitat diversity also increased. At the within basin level, 45% of the variation in size class diversity could be explained with habitat diversity.

SUMMARY

When these results are taken in aggregate, a number of patterns emerge. First, a large number of habitats exist in this system that have all the physical attributes required for various size classes of fish, yet are unutilized. We suggest that this is a common occurrence for small populations and has important ramifications for regression-type analyses.

The diversity of habitats changes as a consequence of scale. Within reaches, habitat richness has little influence on localized densities or distributions, suggesting that more continuous measures of habitat variables apply at this scale (Fausch et al. 1988, Moore and Gregory 1988, Heggenes et al. 1991, Horan 1996). As the scale of inquiry increases to the basin-wide level, the diversity of habitats at different reaches and different tributaries can explain a large proportion of the overall diversity of size classes and densities of the population.

Finally, the notion that the largest areas possible provide the greatest amount and quality of habitats appears unwarranted in our case. While the total number of habitats is directly attributable to the overall area of each subbasin fragment (Table 5), the diversity of habitats is not. Indeed, the population showing the highest density and

greatest size class diversity at the basin wide scale (the Willow subbasin) is the smallest fragment in our study. This subbasin shows the highest diversity and richness of habitats at all spatial scales (Table 5).

We suggest that a landscape approach (Forman and Godron 1986, Schlosser and Angermeier 1995) to fish population/habitat associations is a better approach to understanding the ecological requirements and conservation practices for populations than traditional fine-scale approaches. This level is necessary because of the ontogeny in habitat use characteristic of most fish populations (Werner and Gilliam 1984). Finally, when dealing with rare or declining population, using statistical analyses that provide discrete categories for habitat use based on linear combinations of continuous variable seems particularly useful, given that the populations may often not be at carrying capacity, but rather are reflecting larger scale limitations or demographic stochasticity patterns.

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Table 1. Variables associated with the presence/absence of small juvenile (< 80 mm FL) Colorado River cutthroat trout. CV is coefficient of variation.

Variable	Partial R^2	F	P
# Woody Debris Dams	0.0732	3.08	0.0871
Submersed Wood	0.0710	2.90	0.0582
CV of stream width	0.0587	2.31	0.0486
Total Canonical Correlation = 0.190			

Table 2. Variables associated with the presence/absence of large juvenile (81-125 mm FL) Colorado River cutthroat trout. CV is coefficient of variation.

Variable	Partial R^2	F	P
Dace	0.2368	12.10	0.0031
Mean Substrate Size	0.1978	8.38	0.0066
CV Substrate Size	0.1623	7.36	0.0099
CV of Residual Pool Depth	0.1461	5.82	0.0214
Proportion of Stable Banks	0.1063	4.40	0.0428
# of Riffles	0.1052	4.24	0.0468
Elevation	0.0718	2.71	0.0989
CV of Velocity	0.0664	2.35	0.1000
Total Canonical Correlation = 0.6810			

Table 3. Variables associated with the presence/absence of subadult (126-160 mm FL) Colorado River cutthroat trout. CV is coefficient of variation.

Variable	Partial R^2	F	P
Mean Substrate Size	0.1774	8.41	0.0061
Volume of Wood	0.1695	7.75	0.0082
Reach Area	0.1271	4.66	0.0385
CV of Retention	0.1142	4.51	0.0408
# of Rootwads	0.1088	4.39	0.0432
Dace	0.1023	4.22	0.0472
# of Habitat Units	0.0806	2.98	0.0983
Proportion of Stable Banks	0.0726	2.51	0.1023
CV of Stream Width	0.0608	2.29	0.1098
Total Canonical Correlation = 0.6449			

Table 4. Variables associated with the presence/absence of adult (>126 mm FL) Colorado River cutthroat trout. CV is coefficient of variation.

Variable	Partial R^2	F	P
Mean Retention Time	0.2478	12.85	0.0009
# of Rootwads	0.1500	6.71	0.0135
CV of Substrate Size	0.0807	3.25	0.0796
Elevation	0.0744	2.89	0.0876
CV of Maximum Pool Depth	0.0675	2.46	0.0968
# Woody Debris Dams	0.0621	2.32	0.1013
Total Canonical Correlation = 0.5242			

Table 5. Subbasin values showing habitat and fish size class diversity, as well as the total number of habitable units calculated at the reach, stream and subbasin scales. Areas are square meters. Fish Densities are numbers per square meter. HD and FD refer to Simpson's Diversity of habitats (HD) and fish size classes (FD).

Subbasin	Total Area	Total Fish Density	Total Habitats	HD Within Reaches	FD Within Reaches	HD Among Reaches	FD Among Reaches	HD Within Subbasins	FD Within Subbasins
EFBF	136,393	0.07	10,218	2.7	2.2	3.6	2.3	3.6	3.6
WFSF	94,689	0.04	10,204	1.7	2.3	3.7	3.3	3.9	3.6
DAHL	14,290	0.06	952	2.4	2.1	3.6	2.6	3.6	3.9
WILL	13,582	0.14	1,943	2.9	1.8	3.9	2.6	3.9	3.9

CHAPTER III

A COMPARISON OF POPULATION, HABITAT, AND GENETIC CHARACTERISTICS OF COLORADO RIVER CUTTHROAT TROUT IN WILDERNESS AND NON-WILDERNESS STREAMS IN THE UINTA MOUNTAINS

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Abstract

Cutthroat trout (*Oncorhynchus clarki sp.*) have experienced severe declines in the interior western United States as a result of anthropogenic influences. Causes for these declines include the fragmentation and simplification of habitat, introduction of non-native competitors and predators, and over-exploitation of the fisheries (Young 1995). The Colorado River cutthroat trout (*Oncorynchus clarki pleuriticus*), once common in the upper Green River and Colorado River watersheds, is currently limited to less than 1% of its former range and exists in isolated sub-drainages in Colorado, Utah, and Wyoming (Behnke 1992, Young 1995).

Our study objectives were to: (1) compare population and habitat characteristics of the Colorado River cutthroat trout in wilderness vs. non-wilderness streams, and (2) compare genetic characteristics of CRCT in wilderness and non-wilderness. We use these data to speculate on the likely role of wilderness lands in the protection of native cutthroat trout.

Densities of adult CRCT were significantly higher in wilderness reaches than in non-wilderness reaches, while densities of juvenile fish showed the opposite pattern. Lengths and weights of juvenile and adult CRCT were significantly higher in wilderness reaches than in the non-wilderness reaches. Adult habitat quality as measured by the percent pool habitat, percent undercut bank, mean particle size, and mean stream depth was significantly higher in wilderness reaches. Large woody debris and the hydraulic retention of the stream were positively related to juvenile abundance and were both higher in non-wilderness reaches.

Hybridization indices were considered low in all streams of the Uintas. The highest numbers of hybrid individuals were found in streams that were most recently exposed to stocking. Genetic differentiation was highest within streams, with little additional differentiation at larger scales. Some homogenization of the genetic characteristics of north slope Uintas populations may have occurred due to introgression with hatchery fish with a subsequent loss of rare alleles.

Wilderness areas may represent some of the best remaining habitat for native cutthroat trout. Wilderness streams represent some of the highest quality habitat in the Uintas and exhibit minimal fragmentation due to anthropogenic causes. Although streams within the Uintas may not reflect the historic habitat potential for CRCT, wilderness areas may represent some of the last, best opportunities for managing large intact blocks of habitat.

INTRODUCTION

Cutthroat trout (*Oncorynchus clarki sp.*) were once abundant throughout the Columbia and Missouri River basins, the Great Basin of Idaho, Nevada, Oregon, and Utah, and the southern Rocky Mountains (Behnke 1992). Twelve sub-species of cutthroat trout have been described that were once present in the western interior United States. Currently, one of those sub-species is extinct, three are listed as "threatened", as designated under the Endangered Species Act (1973), and the rest are specially designated by various state and federal agencies. The severe declines in

cutthroat trout populations are almost certainly due to anthropogenic influences including the fragmentation and simplification of habitat, introduction of non-native competitors and predators, and over-exploitation of the fisheries (Young 1995).

The fragmentation of watersheds due to impoundment, water diversions, and hostile temperature regimes due to the loss or riparian vegetation has isolated many salmonid populations into stream headwaters, where they formerly existed throughout major river systems (Behnke 1992, Young 1995). These isolated populations have in many cases lost complete population sub-groups whose life history was dependent on their ability to migrate throughout these larger drainages (McIntyre and Rieman 1995). Land management activities such as mining, logging, road building, and grazing have reduced the quality of the remaining habitat, further shrinking the available habitat.

The introduction of exotic fishes may significantly influence salmonid communities through hybridization (Dowling and Childs 1992), competition (Griffith 1988), predation, and the introduction of new parasites and diseases (Krueger and May 1991). Hybridization between native cutthroat and other salmonids such as the rainbow trout (*Oncorynchus mykiss*) may occur when there is gene flow between one species into the gene pool of another species (Carmichael et al. 1993, Krueger and May 1991). If gene flow is large, then adaptive gene complexes that have evolved to permit native species to adapt to local conditions may be compromised, and ultimately, one gene pool may be completely swamped by another. Elevation may play a role in the separation of rainbow and cutthroat where they are naturally sympatric. Hanson (1977) found cutthroat trout occupied the upper portions of streams while steelhead

occupied the lower portions. Cutthroat trout may outcompete rainbow trout at higher elevation reaches of streams (MacPhee 1966, Griffith 1988, Fausch 1989), while rainbows may have a competitive advantage at lower elevation sites.

Competition with non-native brook trout (*Salvelinus fontinalis*) has been hypothesized as part of reason for the decline of native cutthroat trout (Griffith 1972, 1988, Fausch et al. 1988, Varley and Gresswell 1988, Young 1995). Brook trout appear to affect cutthroat trout primarily through interference competition (Thomas 1996), and DeStasso and Rahel (1994) believe that higher stream temperatures may offer a competitive advantage to brook trout. Non-native predators may also affect native cutthroat populations where highly piscivorous fish, such as brown trout (*Salmo trutta*), are introduced.

Cutthroat trout have high catchability rates and are susceptible to over-harvest (Gresswell 1985). Schill et al. (1986) found that Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) were captured an average of 9.7 times/individual during the fishing season in a catch and release section of the Yellowstone River. Given this susceptibility to angling, significant population declines may have occurred, particularly where anglers have easy access to cutthroat populations (Thurow et al. 1988).

As the range of acceptable habitat for native cutthroats declines, the largest intact habitats may exist in wilderness areas or national parks. Wilderness areas and national parks may provide some of the last opportunities for both studying and conserving native cutthroat trout. Gresswell (1995) found that population declines and extirpations of Yellowstone cutthroat trout occurred more often in low-elevation, larger

streams where most human activities including agriculture and resource extraction have occurred. He speculated that the remote nature of high-elevation portions of the native range probably contributed to the preservation of the remaining populations, and that these areas are typically in public ownership. McIntyre and Rieman (1995) observed similar patterns for westslope cutthroat (*Oncorynchus clarki lewisi*), noting that the strongest populations remain largely in roadless and wilderness areas, or national parks.

The Colorado River cutthroat trout (*Oncorynchus clarki pleuriticus*), hereafter referred to as CRCT, was once common in the upper Green River and Colorado River watersheds, but is currently limited to less than 1% of its former range exists in isolated sub-drainages in Colorado, Utah, and Wyoming (Behnke 1992, Young 1995). The species is listed as a Category 2 species by the USDI Fish and Wildlife Service, a sensitive species by the USDA Forest Service, and designated with special management status in Colorado, Utah and Wyoming. Historically, CRCT were free to move throughout many of the larger tributaries to the Green and Colorado systems, but are now primarily restricted to headwater systems located at higher elevations.

Our study objectives were to: (1) compare population and habitat characteristics of CRCT in wilderness vs. non-wilderness streams, and (2) examine the extent of hybridization with rainbow trout in wilderness and non-wilderness. We use these data to examine the likely role of wilderness lands in the protection of native cutthroat trout.

STUDY AREA

The study area was the north slope of the Uinta Mountains, an east-west range on the Utah-Wyoming border (Figure 1, Table 1). The study streams drain north into the Green River above Flaming Gorge Dam. Streams on the north slope of the Uinta Mountains support populations of cutthroat trout, rainbow trout and brook trout. Other fish species in the study area include mountain whitefish *(Prosopium williamsoni)*, mottled sculpin *(Cotttus bairdi)*, mountain sucker *(Catostomus platyrhynchus* Cope) and longnose dace *(Rhinichtyhs cataractae)*.

Management History

Streams on the north slope Uinta mountains have undergone a variety of management activities since European settlement. In the early 1900's, tie drive logging occurred in many streams within the Uintas to supply cross-ties for railroad construction (unpublished data, Wasatch-Cache National Forest). Logging occurred primarily below currently designated wilderness boundaries. Streams that experienced tie-drive logging continue to exhibit poor pool quality, have unstable streambanks, and lack late successional vegetation (Black 1996). Currently, non-wilderness areas on the north slope of the Uintas are managed for timber harvest, oil and gas leasing, grazing, and recreation. An extensive road network exists throughout the Uintas in the non-wilderness area.

All major streams on the north slope have been diverted or dammed to provide water for domestic, municipal, and agricultural use. In the major drainages dams have limited access to other streams throughout the basin. Irrigation diversions are prevalent in all watersheds and may constitute total or partial barriers depending on the season and the type of diversion.

The High Uintas Wilderness Area was established in 1963 and is managed primarily for recreational use and grazing. While there is an extensive trail network within the wilderness, roads constructed prior to the wilderness designation have been closed and obliterated. Recreational uses include hunting, fishing, sightseeing, and packing. An extensive network of high-elevation lakes exists within the wilderness area and many of these lakes have been stocked with non-native salmonids (unpublished data, Utah Division of Wildlife Resources). Some stream stocking of both native and non-native salmonids occurred earlier in the century by horse pack.

To determine if population characteristics differed between wilderness and non-wilderness areas, we identified streams that contained suspected populations of CRCT and which lacked brook trout from stream survey reports (Utah Division of Wildlife Resources, unpublished data; Kevin Johnson, Wyoming Department of Fish and Game, personal communication). These watersheds included Dahlgreen Creek (DAHL), East Fork Blacks Fork River (EFBF), West Fork Smith's Fork River (WFSF), and Willow Creek (WILL) (Figure 1). We used watersheds without non-native brook trout to eliminate confounding effects that brook trout may have had on CRCT. However, analyses were conducted on populations from 10 streams in the Uintas that

included streams with high potential for hybridization, given fish stocking practices (Table 1).

METHODS

Habitat Survey

During summer 1993 and 1994, we surveyed streams at low-summer stream flows. All streams were separated into reaches that were geomorphically distinct based on changes in gradient, substrate particle size, sinuosity and valley confinement (Rosgen 1985, Horan 1996). A 100 m subreach was randomly chosen for sampling from each reach for a total of 89 subreaches. The gradient of each reach was calculated from United States Geological Survey 1:24000 maps and then verified in the field with a clinometer.

We classified habitats occurring within each subreach into discrete units of pools and riffles (Hawkins et al. 1993). In each unit, we measured length, mean wetted width, mean depth, and the total length of undercut bank, if the undercut was >10 cm. We classified pools according to their formative feature (e.g., debris, plunge, scour, beaver dam) and recorded maximum depth and tail depth. Banks were categorized as stable or unstable, and the length in each category was measured. Stable banks were usually vegetated and characterized by a strong, well developed root system that helped to prevent excessive erosion and sloughing. Unstable banks were not well vegetated, showed signs of collapse and had the potential to add large amounts of fine sediments to the stream.

Within each subreach we quantified the amount of large woody debris present by assigning wood into the following classes: (1) single pieces (>10 cm diameter and 3 m long), (2) aggregates (>2 single pieces in contact with one another and trapping debris), or (3) rootwads. Wood that was at least partly in the bankfull channel was measured. The length, diameter at breast height, and percent submergence was measured for each category. Height was recorded for aggregates and root wads. The number of single pieces in each aggregate was also recorded.

We randomly chose two fast units (riffles, runs) and two slow units (pools) in each subreach to measure particle size distribution, velocity, and hydraulic retention. We divided each of the four units into thirds by two transects, sampled twenty particles along each transect, and measured the longest axis of each particle to the nearest one-half centimeter. Velocity and hydraulic retention were measured by continually applying fluorescent dye into the top of the habitat unit until it was concentrated with color. We measured velocity as the time it took the dye to go from the top to the bottom of the habitat unit, and hydraulic retention as the time it took the thalweg to be clear of dye at the bottom of the unit.

Population Survey

Densities and size structure of CRCT were sampled in each of the subreaches immediately before we conducted the habitat survey. We blocked the upstream and downstream ends of each subreach with nets to prevent fish from leaving the sampling

area. We collected fish with a Smith-Root Model 7 backpack electroshocker using a total depletion method (i.e., several passes were made until less than five trout were caught on the final pass). Young-of-year were not collected. After each pass, we weighed each trout to the nearest gram and measured fork length (FL) to the nearest millimeter. Other fish species were identified and counted.

Genetic Methods

Fish were collected using both electroshocking and angling techniques, depending on the distance from road access. We sampled five streams at two or more locations along an elevation gradient, noting the distance from stocking access on field maps (Table 1). Fish were euthanized with an overdose of MS-222 (methyl sulfonate-tricane) and were flash frozen whole in liquid nitrogen in the field.

Samples of skeletal muscle, liver, and eye were placed in AAT grinding buffer (0.247 g pyidoxal-5-phosphate in 1000 ml of distilled water [R. Williams, personal communication, Clearwater Genetics, Boise, Idaho]) and homogenized. Samples were then prepared and electrophoresed using horizontal starch gels, with subsequent enzyme visualization using stains and buffer systems of Allendorf et al. (1977) and Morizot and Schmidt (1990).

We identified 10 loci that were diagnostic between CRCT and rainbow trout and also 9 polymorphic loci (loci for which the most common allele has a frequency of less than 0.95) from 17 enzyme systems and 37 presumptive gene loci in muscle and liver tissue (Bischoff 1996) . Type A (pure) (Binns 1977) hatchery CRCT (N=30; Daniel

Hatchery, State of Wyoming) and pure rainbow trout (N=30; Fisheries Experiment Station, Logan, Utah) were used to determine allele frequencies of the putative diagnostic loci in each species. We then scored the 10 diagnostic loci for 190 wild CRCT to assess hybridization. We also used the 9 polymorphic loci from wild CRCT to assess the degree of genetic differentiation in populations across the north slope of the Uinta Mountains. Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) have been introduced into north slope Uinta streams in Utah and Wyoming (unpublished data, Utah Division of Wildlife Resources). Because of the lack of sufficiently clear diagnostic loci between Yellowstone and Colorado River cutthroat trout, we could not determine if Yellowstone cutthroat trout alleles were present in the trout populations we sampled.

Data Analysis

Population and Habitat Data

We determined cutthroat trout age from a length-frequency histogram of all captured trout (n = 1967). We used two age classes in the analyses: juvenile (<125 mm FL; n = 819) and adult (>125 mm FL; n = 1148). We determined the density (#/100 m^2) of juvenile and adult trout by calculating the mean density of each subreach, and then calculated an overall mean of the subreaches in both wilderness and non-wilderness reaches. Juvenile and adult densities were $\log_{10}(X + 1)$ transformed to meet the assumption of normality required for parametric statistics. We estimated stream population size by calculating the mean density of fish per meter

juveniles and adults) in a subreach and multiplying that value by the length of the reach. We summed all reach totals within a stream. We used the SAS System for Microsoft Windows, version 6.1 (SAS 1993), to perform all population and habitat statistical analyses; using a significance level of $P < 0.10$. To test differences in fish density, fish length and weight, and habitat characteristics between wilderness non-wilderness reaches we used a one-way analysis of variance (ANOVA) to test whether the means of each variable were different. We used a similar approach to determine differences in length and weight for both juvenile and adult CRCT.

In previous work we determined that a suite of variables including undercut banks, percent of pool habitat, large woody debris, mean depth, hydraulic retention, residual pool depth, and mean substrate size were important in explaining juvenile and adult fish density (Horan 1996). We used these variables in an index that measured the relative amount of complexity available in each reach (Horan 1996). Complexity was determined by calculating mean complexity of each subreach, then calculating an overall mean of all subreaches in the wilderness and non-wilderness categories. ANOVA was used to test whether complexity was different between wilderness and non-wilderness.

Genetic Data Analysis

To test for the degree of hybridization between the two species, we used a hybrid genetic index developed by Campton and Utter (1985) to distinguish between steelhead trout (*Oncorhynchus mykiss*) and coastal cutthroat trout (*Oncorhynchus clarki clarki*). This hybrid index assesses the likelihood of hybridization by measuring

the relative probability that the composite genotype for each fish arose from random mating within either species. The index values range from zero (0.0) to one (1.0), with values close to 0.0 or 1.0 indicating that the individual has a very high probability of being a cutthroat trout or rainbow trout, respectively. If many individuals scored near 0.5, this would provide strong evidence for ongoing hybridization (Campton and Utter 1985). The index is based on the average allele frequencies for loci resolved in muscle and liver tissue in the pure hatchery populations of the two species.

Sampled populations can have different allele frequencies for a polymorphic locus, but the differences may go undetected if small sample sizes are used (Baverstock and Moritz 1990). In addition, allele frequency differences may be found in the sample that are not found in the population as a whole. In this study relatively small sample sizes of hatchery fish were used to detect diagnostic differences between the two species. Hatchery fish have been found to have reduced genetic variation from wild populations (Allendorf and Leary 1988). Due to these three problems it is possible that some diagnostic differences may have gone undetected and allele frequencies for diagnostic loci may be incorrect. To address this problem, cut-off values for the hybrid index of HI < 0.25 (cutthroat trout) and HI > 0.75 (rainbow trout) were chosen rather than less stringent cut-off values to prevent the misclassification of individuals as hybrids.

Each individual was assigned to one of three subgroups based on values of the hybrid index where (HI) scores: HI < 0.25 = cutthroat trout (CT), HI > 0.75 = rainbow trout (RT), and HI from 0.25 to 0.75 = hybrids (HB). These cut-off values were chosen

because a hybrid index of 0.25 would be the result of a first generation hybrid individual backcrossed with a pure cutthroat trout. Therefore, values less than 0.25 identify a fish with at least two generations of backcrossing with pure cutthroat trout (i.e., an F1 generation hybrid bred with a pure cutthroat and the resulting offspring also bred with a pure cutthroat). Campton and Utter (1985) used index scores of HI < 0.3 (CT), HI > 0.8 (Steelhead), and HI from 0.3 to 0.8 (HB) to partition these two species and hybrids.

We tested for heterogeneity and genetic variance among all of our sample populations. We used a hierarchical analysis of f-statistics to compare differentiation at three levels; sample site to stream, stream to watershed, and watershed to north slope Uintas. The reduction of heterozygotes in a subpopulation due to random genetic drift is measured by f_{st}, which can be used as an index of genetic differentiation among populations. Values of 0 - 0.05 indicate little differentiation, 0.05 - 0.15 is considered moderate differentiation, and values greater than 0.25 are considered to represent high differentiation (Hartl 1987). Heterogeneity tests were calculated using the BIOSYS-1 computer program (Swofford and Selander 1981).

RESULTS

Population and Habitat Characteristics

Both adult and juvenile densities were significantly different between wilderness

and non-wilderness reaches. Adult densities were higher in wilderness reaches, while juvenile densities were higher in non-wilderness reaches (Table 2). Characteristics of individual fish were also different between wilderness and non-wilderness. Both adult and juvenile lengths and weights were significantly higher in wilderness than non-wilderness (Table 2).

Habitat variables that were positively related to adult density included percent undercut banks, percent pool habitat, dominant substrate particle size, and mean depth (Horan 1996). The mean of the percent undercut banks was nearly 2.5 times greater in wilderness than in non-wilderness (Table 2). A plot of adult density against undercut bank, in WFSF, showed the importance of that habitat type to the WFSF population (Figure 2). Three reaches located above the wilderness boundary are particularly important, as they had high percentages of undercut bank and supported the highest density of adults. Thirty-four percent of the adults in WFSF live above the wilderness boundary, yet the wilderness area is only 15% of the entire WFSF sampling area. The mean of the percent of pool habitat, mean of the dominant particle size, and mean depth were also greater in wilderness reaches than in non-wilderness reaches (Table 2). Variables that were related to juvenile abundance included pieces of large woody debris, and mean depth (Horan 1996). The mean number of pieces of large woody debris was significantly higher in non-wilderness areas than in wilderness areas (Table 2). Mean depth was significantly higher in the wilderness stream reaches.

Mean values of the habitat complexity index were significantly higher for the

wilderness stream reaches. The EFBF was the most complex section, followed by the DAHL (all non-wilderness) , the WFSF, and WILL (all non-wilderness) (Figure 3). Complexity was positively related to adult trout abundance ($r = 0.94$, $P < 0.06$) and density ($r = 0.92$, $P < 0.08$), but these tests were not statistically significant under sequential Bonferroni criteria (Horan 1996). Complexity was not related to juvenile abundance or juvenile density.

Hybridization

We detected 10 diagnostic loci that discriminate hatchery populations of CRCT from hatchery populations of rainbow trout (Table 3). Idh-1 and Mpi are the only linked loci in the study. Complicated banding patterns from null alleles for Ck-1, Pgm-2, and G_3PDH did not permit the discrimination of heterozygotes from homozygotes, but data for these loci were retained with all individuals scored as homozygotes. The frequencies of alleles at all 10 loci were used in the hybrid index. Loci Ada-1 and Me-1 had alleles with a frequency of zero or one for each species and were considered fixed or marker loci.

The hybrid indices for individual fish, using the 10 diagnostic loci, revealed no hybrid index higher than 0.52, suggesting no backcrossing between hybrids and rainbow trout. One hundred and ninety fish were analyzed: 172 were classified as CT, 18 as hybrids, and zero as RT. Only one sample location, Gilbert Creek's low elevation

site, had a mean hybrid index of 0.25 or higher. All other sample points had a mean index value below 0.25, suggesting that these areas have a high probability of containing relatively pure Colorado River cutthroat trout (Table 1).

We found one hybrid individual at the highest elevation site sampled in Little East Fork Blacks Fork, a number of hybrid individuals in both the lower and upper elevation sites in Gilbert Creek, and four hybrids in South Fork Sheep Creek (Table 1). In all other cases, the number of hybrids and the hybrid index decreased with increasing elevation. In cases where streams were accessible by road, we found evidence of hybrid individuals. Generally, the hybrid index decreased as the distance to stocking access increased (Table 1).

The analysis of hierarchical f-statistics indicated a large differentiation between sample points within streams, no additional differentiation at the stream-to-watershed level, and a small to moderate amount of differentiation at the watershed-to-north slope (total) level using all of the trout in the sample (Table 5). When we used only CRCT that were considered "pure" in the analysis, the pattern remained the same at the site-to-stream level, but there was a moderate amount of differentiation at the stream-to-watershed level, and no additional differentiation across the north slope.

DISCUSSION

Wilderness stream habitats may present some of the last, best opportunities for

managing populations of CRCT. While we caution that recovery and restoration efforts cannot only consider wilderness areas, we believe that wilderness and roadless watersheds may represent important anchoring points for the recovery of CRCT populations on the north slope Uintas. In the Pacific Northwest (USA), wilderness and roadless areas have been identified as important components of the Northwest Forest Plan for the recovery of anadromous fish stocks (Thomas et al. 1993). In many cases they are part of "key watersheds" that serve to provide refuge habitat for native species while the recovery of severely disturbed habitats takes place (Reeves et al. 1995).

High-quality habitats for adult fish appear to be in short supply in many areas that we surveyed on the north slope Uintas. Although habitat within the Uintas wilderness and roadless areas is by no means "pristine", habitats appear to remain largely intact and are high quality in the wilderness reaches that we surveyed. In particular, important adult habitat characteristics such as undercut banks, and mean depth were significantly better in wilderness streams. This quality appears to be reflected in the high densities of adult cutthroat that inhabit these areas, and the condition (length and weight) of individual CRCT relative to fish we observed in non-wilderness streams. In areas outside wilderness where the quality of adult habitats was diminished, we saw reduced numbers of adult fish and a predominance of sub-adult fish in the survey.

The implications of the disparity in habitat quality between wilderness and non-wilderness may be significant. Shaeffer (1981) estimated the minimum number of

breeding individuals in a closed population to be 50 to prevent excessive rates of inbreeding and 500 to maintain genetic variation. Nelson and Soule (1987) concluded that in fish, these numbers may be closer to 500 and 5000 respectively. Viability analyses for bull trout indicate that substantial risks of extinction were projected to occur when there were less than 100 redds or 2000 individuals within a closed population (Rieman and McIntyre 1993). Looking at total population estimates in north slope Uinta streams (Horan 1996), we estimated that two stream fragments (WFSF and EFBF) had populations in excess of 2000 individuals, and only one patch (EFBF) had an estimated total population of over 8000 individuals, and an adult population over 6000 individuals (Table 4). In the West Fork Smiths Fork, high quality habitat and the associated high densities of adult fish in wilderness appear to make a disproportionately high contribution to the overall population of the stream, while over 95% of the EFBF patch is within the wilderness. If existing extinction models for other salmonids apply to CRCT, then there may currently be few watersheds on the north slope with the ability to provide for long-term population persistence and these are probably associated with the presence of wilderness.

The lack of hybridization we observed throughout wilderness and non-wilderness reaches is surprising given the past levels of non-native stocking that have occurred on the north slope of the Uintas. Virtually every accessible water body has been stocked at one time with mixtures of rainbow trout, Yellowstone cutthroat, and brook trout. As late as 1971 it was believed that "pure" CRCT were extinct across the

orth slope of the Uintas, except for Blacks Fork (unpublished data, Wasatch-Cache National Forest). Stream fisheries surveys during this time period reported rainbow trout, brook trout, and hybrid cutthroats except for isolated sections of streams within the Uintas such as the East Fork Blacks Fork where biologists noted the possibility that CRCT may exist in some of the smaller side drainages (unpublished data, Utah Division of Wildlife Resources, Northern Region 1974). During the 1980's and 1990's stocking was no longer practiced in all of our study streams with the exception of Sheep Creek. Both the main fork and the middle fork of Sheep Creek have been stocked annually until 1995 (unpublished data, Utah Division of Wildlife Resources). While elevation and distance to stocking access may influence hybridization, a third component; date of last stocking appears to be more important. This is particularly true in the South Fork of Sheep Creek where mainstem stocking has been frequent. We believe that the continuous stocking of fish in Sheep Creek may promote the continued exchange of genetic material between CRCT and rainbow trout. In other streams where stocking has been discontinued we observed low levels of hybridization and CRCT appear to have been re-established in many of the areas that we surveyed. We believe that isolated, remnant sub-populations of CRCT that existed in wilderness areas, and areas with limited road access are most likely responsible for refounding the current populations that we observed. These areas probably represent the best source of genetic material that is currently available on the north slope of the Uintas.

Isolation-by-distance models typically predict that neighboring populations

should exhibit greater similarity than more geographically distant populations (Hartl and Clark 1989). Our analysis indicated that the highest differentiation occurred between sites within streams and a much smaller amount of differentiation occurred at larger scales. One possible explanation is that hybridization and the subsequent introgression with rainbow trout may have homogenized the genome in these streams. Allendorf and Phelps (1981) found changes in allele frequencies in wild rainbow trout when hatchery fish were introduced, while Reisenbichler and Phelps (1989) found low levels of genetic differentiation in steelhead trout within and among drainages where hatchery stocking had occurred. Hatchery fish typically have little genetic variation (Allendorf and Leary 1980) and when they are stocked, similar genotypes are placed in streams. While localized stocking within streams may cause greater differentiation at that level, there may be little differentiation at higher scales. The consequences of this stocking may be that locally evolved gene complexes may be lost with the subsequent loss of locally adapted populations (Allendorf and Leary 1988). While hybridization in the Uintas currently appears to be low in most streams, we may have already lost locally adapted gene complexes in some areas.

Current habitat conditions for many resident salmonids in the interior western U.S. differ markedly from those for anadromous fish in the Pacific Northwest United States. Watersheds that were once connected throughout larger river basins like the Green River are now disjoint due to physical diversions and barriers. Large, fluvial fish that once moved freely throughout the basin can no longer move between basins and

have in many cases disappeared (Behnke 1992, Young 1995). Stream resident fish are the dominant form in most remaining drainages and have limited potential for moving between watersheds and in some cases within watersheds. In the Uintas, diversion sites and reservoirs typically occur within a relatively short distance of the wilderness boundary. Relatively large, connected watershed fragments exist only above these barriers in many areas. The opportunity to establish large, connected "meta-populations" (Hanski and Gilpin 1991, Rieman and McIntyre 1993) may be difficult given the current degree of fragmentation. For example, Rieman and McIntyre (1993) believe that large rivers or lakes have the highest potential for supporting large populations of fluvial bull trout (*Salvelinus confluentus*). They believe that all habitats must be present for bull trout to persist and the population sufficiently large, or with enough sub-populations to survive catastrophic failure. On the north slope Uintas, there are few watersheds over 200 km^2 that are not fragmented. Most of these remaining watersheds have their origin in wilderness and have a significant wilderness component. These remaining watersheds should be surveyed to determine the extent and characteristics of current fish populations and their potential as recovery areas for CRCT. However, because non-native competitors (brook trout) are present in many of these watersheds, opportunities for establishing metapopulations may be limited unless these competitors are removed.

Conserving the remaining populations of native salmonids in the western United States has become increasingly important as populations continue to decline.

Conservation strategies must focus on identifying the extent and makeup of existing populations, the status of habitat in both current and historic ranges, and the potential for restoring populations where possible. Past efforts to restore inland salmonids have generally isolated small populations above impassable barriers to maintain genetic purity (Young 1995). The danger with this strategy is that persistence of these populations may be limited due to small population numbers and limited habitat area. Both demographic and stochastic risk of extinction may be high. If we are to succeed with the recovery of native cutthroats like the CRCT, then we will need to expand our focus to include the largest, connected watersheds available. We believe that wilderness areas like the High Uintas Wilderness provide the best hope to anchor this recovery.

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Table 1.--Stream name, sample sizes, altitude, approximate distance to a road, number of hybrids in sample, and mean hybrid index (HI).

Stream	N	Altitude(m)	Distance to Road (m)	Hybrid Number	HI
EFBF	15	2959	3500	0	0.07
LEFBF L	9	2928	1500	1	0.05
LEFBF H	6	3233	7000	1	0.14
HF L	5	2867	<500	1	0.11
HF H	9	3203	11000	0	0.11
DAHL L	10	2623	4000	0	0.14
DAHL M	10	2776	<500	1	0.12
DAHL H	12	2959	4000	0	0.02
L GIL	6	2959	1500	0	0.02
GIL L	9	2806	<500	5	0.25
GIL M	10	2928	<500	0	0.05
GIL H	6	2930	<500	2	0.20
AC	11	2959	3000	1	0.10
WFSF L	11	2745	<500	2	0.15
WFSF ML	11	2837	<500	0	0.02
WFSF MH	12	2898	1000	0	0.05
WFSF H	12	3294	8000	0	0.02
NFSC	15	2806	1000	0	0.09
SFSC	10	3020	6500	4	0.16

East Fork of Black's Fork (EFBF); low Little East Fork of Black's Fork (LEFBF L); high Little East Fork of Black's Fork (LEFBF H); Archie Creek (AC); low West Fork of Smith's Fork (WFSF L); middle low West Fork of Smith's Fork (WFSF ML); middle high West Fork of Smith's Fork (WFSF MH); high West Fork of Smith's Fork (WFSF H); low Gilbert Creek (GIL L); middle Gilbert Creek (GIL M); high Gilbert Creek (GIL H); Little Gilbert Creek (L GIL); low Dahlgreen Creek (DAHL L); middle Dahlgreen Creek (DAHL M); high Dahlgreen creek (DAHL H); low Henry's Fork (HF L); high Henry's Fork (HF H); North Fork of Sheep Creek (NFSC); South Fork of Sheep Creek (SFSC).

Table 2. Comparison between wilderness and nonwilderness stream reaches. All comparisons are significant ($P < 0.10$) except residual pool depth and juvenile density.

Variable	Wilderness n = 34 Mean	(se)	Nonwilderness n = 54 Mean	(se)
Undercut banks (%)	17.55	(2.76)	7.20	(.74)
Pool habitat (%)	29.29	(2.62)	22.78	(1.37)
Large woody debris (PCs)	2.77	(.66)	5.39	(.86)
Particle size (mm)	160.83	(12.86)	134.07	(5.00)
Depth (m)	.22	(.01)	.15	(.01)
Hydraulic retention (s/m)	13.07	(2.39)	34.47	(4.47)
Residual pool depth (m)	.26	(.02)	.27	(.01)
Habitat complexity index	95.26	(5.14)	85.21	(2.51)
Juvenile density (#/100m^2)	1.96	(.27)	3.80	(.87)
Adult density (#/100m^2)	6.17	(.77)	1.47	(.19)
Juvenile length (mm)	100.40	(1.87)	92.89	(2.04)
Adult length (mm)	185.06	(2.08)	161.86	(2.61)
Juvenile weight (gm)	13.06	(.63)	9.65	(.54)
Adult weight (gm)	72.59	(2.37)	48.09	(2.29)

Table 3. Allele frequencies at 10 diagnostic loci in Colorado River cutthroat trout and rainbow trout reference populations.

Locus	Allele	Colorado River Rainbow trout	cutthroat trout
ADA-1	a	0.00	1.00
	b	1.00	0.00
CCK-1	null	1.00	0.00
	b	0.00	1.00
EST-2	a	0.98	0.00
	b	0.02	1.00
G_3PDH	null	0.00	1.00
	b	1.00	0.00
IDH	a	0.83	0.00
	b	0.17	1.00
ME-1	a	0.00	1.00
	b	1.00	0.00
MPI	a	0.00	0.19
	b	0.98	0.81
	c	0.02	0.00
PEPB-1	a	0.02	1.00
	b	0.98	0.00
PGM-2	a	0.89	0.02
	null	0.11	0.98
SOD-1	a	0.86	0.00
	b	0.14	1.00

Table 4. Population characteristics of Colorado River cutthroat trout among patches in the Uinta Mountains; Willow, Dahlgreen, West Fork of Smiths Fork (WFSF), and East Fork of Blacks Fork (EFBF). Standard error is in parentheses.

	Population size (no.)		
Patch	Total	Juvenile	Adult
Willow	1977	1725	252
Dahlgreen	838	714	124
WFSF	3136	1502	1634
EFBF	8229	2191	6038

Table 5. Hierarchical f-statistics for all 19 wild populations of (a) Colorado River cutthroat trout and (b) populations containing no hybrid individuals as defined by the hybrid index.

Comparison			
X	Y	f_{XYa}	f_{XYb}
Site	Stream	0.261	0.256
Stream	Watershed	-0.003	0.172
Watershed	Total	0.078	-0.021

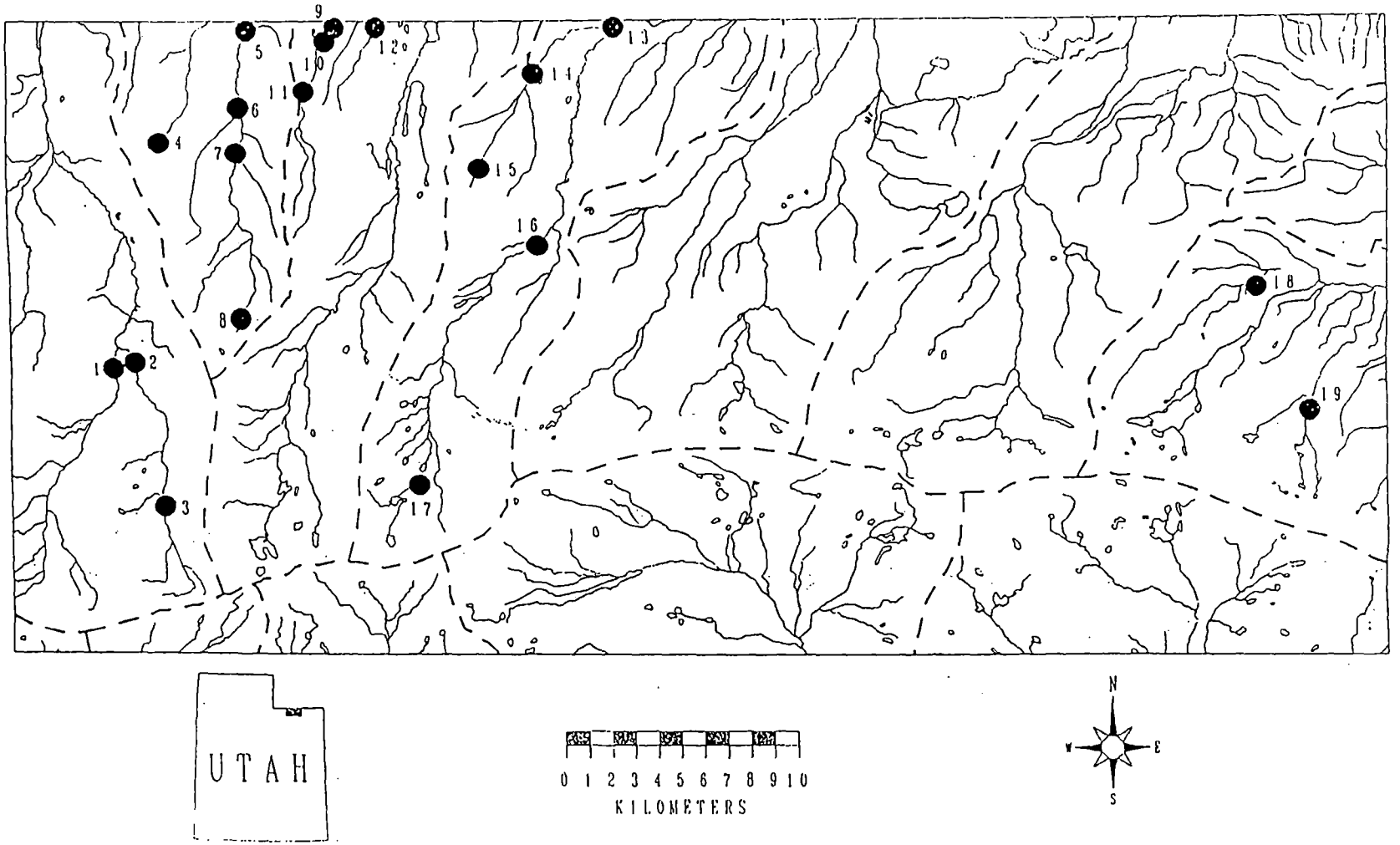

Figure 1. Map of the study area including the genetic sampling sites and the habitat and population surveys.

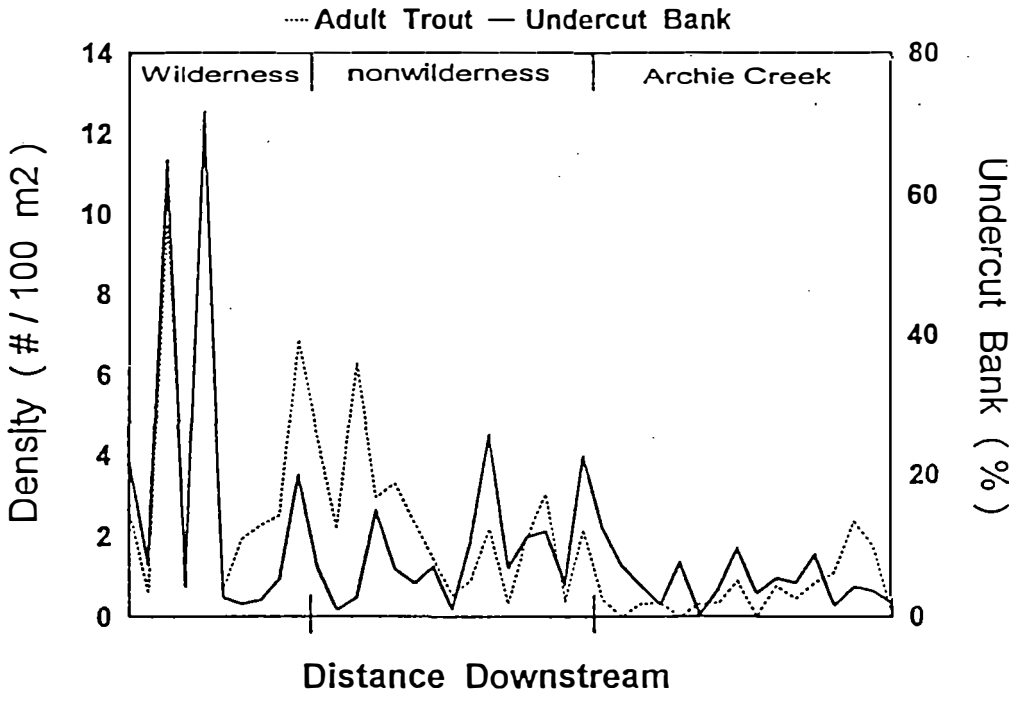

Figure 2. Density of adult cutthroat trout in relation to undercut banks in reaches of the West Fork Smith's Fork. WFSF consists of three sections; the High Uintas Wilderness, mainstem WFSF below the wilderness boundary, and Archie Creek which is a tributary to WFSF.

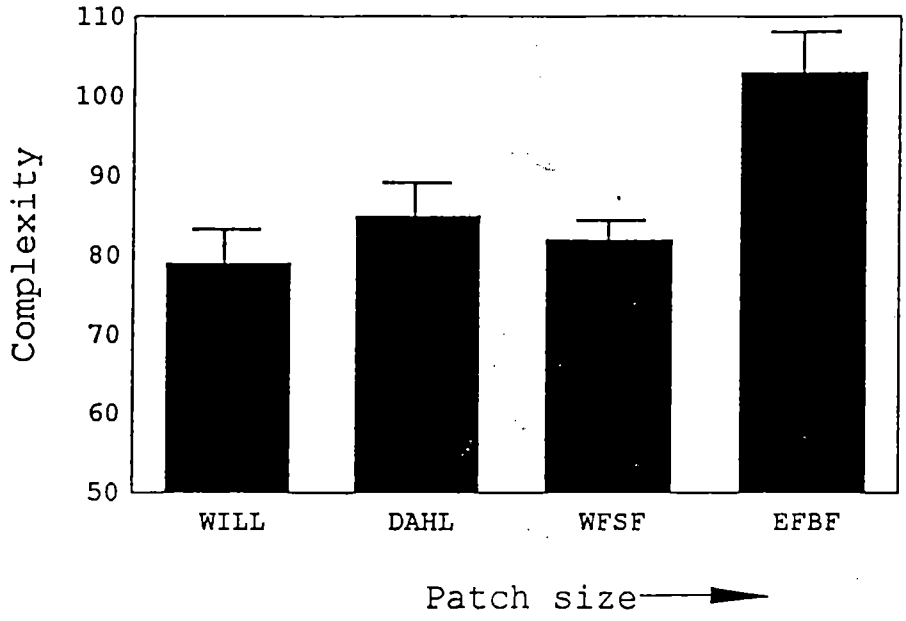

Figure 3. Habitat complexity among patches using an index based on the Euclidean distance formula. Error bars represent one standard error.

CHAPTER VI

Competitive Interactions Between a Native and Introduced Trout Species in a High Mountain Stream

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Abstract

Populations of the introduced brook trout, *Salvelinus fontinalis*, have recently become more widespread and abundant in western North American streams, possibly at the expense of native Colorado River cutthroat trout, *Oncorhynchus clarki pleuriticus*. We examined the intensity and potential mechanism of competition between these species.

Feeding experiments in laboratory stream channels showed that cutthroat trout feeding efficiency decreases in the presence of brook trout. Decreased feeding efficiency appeared to be due to interference, as cutthroat trout were inactive in the presence of brook trout. Evidence for interference competition in the feeding experiments was also given by the fact that brook trout feeding efficiency was lower than the feeding efficiency of cutthroat trout. The decreased feeding efficiency of cutthroat trout in the presence of brook trout was due to decreased attack rates by cutthroat trout, and was not due to attacks and consumption of the food items by brook trout.

A field enclosure experiment, in which riffle-pool sections of a stream were isolated by fencing, was performed to determine if the presence of brook trout had a negative effect on the growth, fat content, and diet of cutthroat trout. Cutthroat trout fat levels were significantly lower in the presence of brook trout. The growth of cutthroat trout was not significantly different in the presence and absence of brook trout, but there was a trend for lower growth of cutthroat trout in the presence of brook trout. Diet

choices and total biomass of prey consumed by cutthroat trout in the field experiment and in a survey of three streams were not affected by the presence of brook trout.

The observed decreased feeding efficiency of cutthroat trout in the presence of brook trout may be the mechanism responsible for significantly decreased fat levels during the relatively short, summer growing season and may result in reduced population sizes due to high overwinter mortality and delayed sexual maturity.

INTRODUCTION

The importance of competition has been a controversial issue in ecology for several decades (Wiens 1977, Schoener 1982, 1983, Connell 1983), with much of the evidence considered to be circumstantial (Pianka 1981). Interspecific competition has not been considered to be an important mechanism regulating herbivorous insect communities (Strong 1983). Interspecific competition also has been considered unimportant in systems with a variable environment or in systems where predation is strong (Wiens 1977, Schoener 1982). However, interspecific competition has been found to be an important mechanism structuring rocky intertidal communities (Menge and Sutherland 1976, Underwood 1978), freshwater lakes (Lynch 1978, Werner and Hall 1976, 1977, Brown 1982, see Schoener 1983 and Connell 1983 for reviews), and various terrestrial plant and animal systems (Werner 1977, Price 1978, Dunham 1980, see Schoener 1983 and Connell 1983 for reviews).

Competition occurs when two or more organisms prevent one another from

obtaining resources (Pianka 1981). Two forms of competition can occur, interference (direct) competition and exploitation (indirect) competition. Interference competition occurs when one individual denies another individual access to resources by fighting, poisoning, or intimidating to improve its competitive position (Levine 1976, Schoener 1983). Exploitation competition occurs when individuals consume the same limiting resources and one individual, by consuming those resources first, prevents another individual benefits gained by those resources (Schoener 1983). Interspecific competition can result in one species exhibiting niche shifts in sympatry (Pianka 1981) or expansion of a species range of habitat or resource use in the absence of a competitor (Diamond 1975). Species that have not evolved together may also have greater ecological overlap in food type and microhabitat use because there has been no opportunity for natural selection to produce differences in resource use (Schoener 1983, Fausch 1988). Greater ecological overlap in food type and microhabitat use may then lead to a higher tendency to compete. Inland cutthroat trout, *Oncorhynchus clarki*, that evolved with few or no other fish species, particularly other salmonid species, may have a higher tendency to compete with introduced species.

Many introduced salmonids have been thought to interact negatively with native fish species (Fausch 1988, Crowl et al. 1992). However, most studies of interspecific competition between salmonids have not been based on well defined experiments that identify competitive mechanisms (Hearn 1987, Fausch 1988). Indeed, many field studies of interspecific competition between salmonids and other exotic fish species have simply compared spatial distributions and diet composition of allopatric and

sympatric populations (Nilsson 1963, Nyman 1970, Andrusak and Northcote 1971, Griffith 1974, Nilsson and Northcote 1981, Glova 1987, Tremblay and Magnan 1991, Glova et al. 1992, McIntosh et al. 1992). Many of these studies concluded that interactive segregation occurs among sympatric populations, in which niche shifts by one or both species results in reduced overlap of resources (Andrusak and Northcote 1971, Fausch 1988). Experimental manipulations in the field and in simulated laboratory streams have been used to examine interactions between salmonids as well (Schutz and Northcote 1972, Fausch and White 1981, 1986, Cunjak and Green 1984, 1986, DeWald and Wilzbach 1992, DeStaso and Rahel 1994), but many of these studies were not designed to reveal competitive mechanisms.

Recent introductions of brook trout, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, in the last 100 years throughout western North American streams have been linked to the decline of several subspecies of cutthroat trout (Moyle and Vondracek 1985, Gerstung 1988, Griffith 1988). Brook trout were stocked in many of the small, high mountain streams of the Colorado River basin and may have altered fish communities in these streams (Binns 1977). These stocking programs appear to have resulted in increasing numbers of brook trout and decreasing numbers of cutthroat trout in at least some streams (Binns 1977). Colorado River cutthroat trout, *Oncorhynchus clarki pleuriticus,* is considered a rare subspecies and its decline is probably due to several factors including habitat loss, as well as the introduction of nonnative salmonids (Martinez 1988). In this study, we investigated potential competitive interactions between Colorado River cutthroat trout and brook trout. Interspecific

competition between cutthroat trout and brook trout should be high in the summer when food and space are limiting (Griffith 1988).

The first objective of this study was to determine if brook trout affected the diet of cutthroat trout in the field. The second objective was to determine if brook trout affected the feeding efficiency and behavior of cutthroat trout in a laboratory setting. The final objective was to determine if brook trout affected cutthroat trout under natural conditions in a manner consistent with laboratory behavioral observations. In a field enclosure experiment, we measured growth, lipid deposition, and diets of cutthroat trout, which are known to affect fish survival.

STUDY SITE

The field survey was conducted in Gilbert Creek, Little Gilbert Creek, and Steel Creek. All three streams are small, first- and second-order streams located in the Uinta Mountains Wyoming-Utah, USA. The fish assemblage in Gilbert Creek and the lower portion of Little Gilbert Creek consisted of cutthroat trout, brook trout, and mottled sculpin, *Cottus bairdi*. The fish assemblage in Steel Creek and the upper portion of Little Gilbert Creek consisted of cutthroat trout and mottled sculpin. Brook trout were introduced between 1940 and 1950. The main substrate in the study areas was gravel-cobble with some boulders. Gilbert Creek has an average baseflow width of 3 m and Steel Creek and Little Gilbert Creek have an average baseflow width of 1.5 m. Summer temperatures in the study areas can range from 7 to 21°C during a 24-h period. The

riparian vegetation was moderately dense and mostly consisted of willow, *Salix* spp., with an occasional lodgepole pine (*Pinus contorta*).

METHODS

Diet Survey

Cutthroat trout diets and diel feeding patterns were assessed in streams with and without brook trout. Diets of cutthroat trout were used to determine (1) if the types of prey consumed and the time of day (dawn, midday, or dusk) prey are consumed by allopatric cutthroat trout differed from those sympatric with brook trout and (2) if the total biomass of prey consumed by allopatric cutthroat trout differed from cutthroat trout sympatric with brook trout.

There were three streams sampled for this survey, Gilbert Creek and the lower reach of Little Gilbert Creek, which contained sympatric populations, and Steel Creek and the upper reach of Little Gilbert Creek, which contained allopatric populations. A dawn (0600-0800), midday (1500-1700), and dusk (2100-2300) sample was taken for each stream once during the summer of 1993. Gilbert Creek was sampled on 11-12 July, Little Gilbert Creek was sampled on 21-22 August, and Steel Creek was sampled on 1-2 September. Ten cutthroat trout were electrofished from the stream during each sampling time, and fish were weighed to the nearest 0.01 g and measured to the nearest 0.1 mm. Cutthroat trout ranged in sizes from 7.0 cm to 23.0 cm. Stomach contents of the fish were evacuated with a modified syringe that forced water into the digestive tract, resulting in regurgitation. Diets were preserved in 95% ethanol. To

relate fish diets to food availability, drift samples were taken during each sampling time. Two drift nets (0.46 m x 0.25 m) were set in riffle areas that were not disturbed by electrofishing approximately 6 to 8 h before each sampling time. Drift nets were pulled from the stream at the beginning of each sampling time and preserved in 95% alcohol. Diets and drift samples were later identified, counted, and measured in the laboratory. Diets and drift were converted to biomass using regression equations relating prey length to prey mass (Rogers et al. 1976, Smock 1980, and C. Hawkins *unpublished data*). To determine if cutthroat trout sympatric with brook trout differed in prey use from allopatric cutthroat trout, biomass of prey in the diets and drift were converted to Chesson's Alpha (Chesson 1978). Chesson's Alpha is defined as:

$$\alpha_i = (r_i / p_i) / \sum r_i / p_i$$

where r_i is the proportion of items of food type *I* in the consumer's diet and p_i is the proportion of items of food type *I* in the environment. A two-way ANOVA comparing fish treatment (allopatric and sympatric cutthroat trout) and time of day (dawn, midday, and dusk) was used to analyze Chesson's Alpha for each of the prey categories (Ephemeroptera, Trichoptera, Diptera larvae, other aquatics, and terrestrials). A two-way ANOVA was also used to determine if the total biomass of prey consumed differed between the allopatric and sympatric populations of cutthroat trout and time of day. The total biomass was log transformed to normalize the data. The significance level for all analyses reported was set *a priori* at 0.10 due to low replication.

Laboratory Feeding Experiment

We performed a laboratory experiment in artificial stream channels during the fall of 1993. We designed the experiment to determine (1) if cutthroat trout feeding efficiency changed when brook trout were present and (2) if interference or exploitation was the most probable mechanism for observed effects.

Feeding experiments were conducted in flowing, oval stream channels. The stream tanks were divided into two sections (3.25 m x 0.61 m, depth = 0.5 m) with average velocities of 0.93 ± 0.015 m/s (± 1 SD). Black plastic curtains were placed on both the inside and outside of the stream tanks to prevent interference from outside light and activity. Viewing windows were cut in the plastic so that an individual could observe feeding interactions by looking down on the fish while minimally disturbing the fish. Six concrete bricks (0.2 m x 0.1 m) were placed into each section to allow cover and resting areas for the fish. A plastic feeding tube was placed at the upstream end of each section and could be reached from inside the tank. Temperatures ranged from 13-17°C and simulated daytime summer temperatures in Uinta mountain streams, from which the experimental fish were derived. A 12-h dark/12 h-light photoperiod (set by timers) was used during experiments. In addition, red lighting was used during 1730-1830 to simulate evening lighting conditions. Fish used in the experiment were collected by electrofishing streams located in the Uinta Mountains. Brook trout were collected from Gilbert Creek; cutthroat trout were collected from Steel Creek, Utah. Cutthroat trout were not taken from Gilbert Creek because they have hybridized with rainbow trout, *Oncorhynchus mykiss* (Bischoff 1995) in that stream. Fish were held in flowing circular tanks for approximately 1 mo before experiments began.

In the experiments, we placed two fish of similar length in each tank, either two cutthroat trout or one cutthroat trout and one brook trout. Each treatment was replicated five times. Fish length ranged from 82 to 159 mm, with no more than a ± 10 mm difference between pairs. One cutthroat trout in the cutthroat-only treatment was fin clipped so that individual fish could be identified. There was a 2-d acclimation period before the feeding trials were started to insure the fish were familiar with the experimental tank and stream flow, and also to control the feeding history of the fish. Fish were fed twice a day during this 2-d period (1000 and 1800). Feeding trials began on the morning of the third day at 1000. Experiments lasted for 3 d, with both morning and evening feeding events (1000 and 1800) recorded for each day. Feeding trials began when a single piece of freeze-dried krill was placed in the feeding tube, which was then washed through the tube and into the water. To determine if cutthroat trout were surface or midwater feeders, krill were released from either the surface of the water column or the middle of the water column. Ten pieces of krill were randomly released one at a time from either the top of the water to simulate surface prey or from the middle of the water column to simulate drifting prey. Another piece of food was introduced either after consumption of the previous food item or after the previous food item traveled the distance of the stream section. A feeding trial was terminated if both fish did not respond to 20 pieces of food. Trout were given additional food at the end of each feeding trial so that starvation did not occur. Individual encounters, attacks, and captures were recorded for each fish for every food item, as well as the fish's position in the water column (middle/bottom).

Results from the feeding experiments were interpreted in terms of encounter rate (no. encounters/no. food items released), attack rate (no. attacks/no. encounters), and capture rate (no. captures/no. attacks). Because the concept of predation can be thought of as a cycle of sequential events (encounter → pursuit → attack → capture), the total probability of a successful predation event or the probability of ingestion of a prey item can be defined by no. captures/no. food items released (O'Brien 1979). A modified version of O'Brien's equation (1979) was used. O'Brien's equation for a predation cycle is defined as:

$$P_I = P_L \times P_P \times P_A \times P_C$$

where P_I = the probability of ingestion of the food item, P_L = the probability of location of the prey, P_P = the probability of pursuit, P_A = the probability of attack, and P_C = the probability of capture. Three of the four components (location = encounter, attack, and capture) of O'Brien's equation were used because pursuit and attack were not measured independently during the experiment. Due to low statistical power (see Table 1), the alpha level was set *a priori* at 0.10 for all statistical analyses. Because a focal fish was not chosen prior to the feeding experiments, the probabilities of feeding efficiency for the cutthroat trout-only treatment were calculated by taking an average of the two fish. A one-way ANOVA did not show any significant differences in probabilities between the two fish in the cutthroat trout-only treatment. A two-way repeated-measures ANOVA was used to determine differences in feeding efficiencies for fish treatment (cutthroat trout only and cutthroat trout + brook trout) and for food item location (surface of mid-water). Repeated measures were taken on each fish

within day (morning and evening observations) for 3 d. A chi-square test was used to compare water column position (middle/bottom) of cutthroat trout in the presence and absence of brook trout.

Enclosure Experiment

General methods.--A field experiment was performed in Gilbert Creek in the summer of 1994 to determine if interspecific competition between cutthroat trout and brook trout affected cutthroat trout growth rates, lipid levels, and diets in a natural setting. Six riffle-pool sequences were sectioned off with plastic fencing (mesh size = 1.0 mm) with at least 12 m between experimental sections (see Table 2 for habitat descriptions). Fences were constructed on 28 June-10 July and extended 1 m into each bank (fences ~ 1 m above water surface). Fences were reinforced with three fence posts and were buried 0.15 m into the sediment to prevent fish movement into and out of the manipulated areas. Each section was electrofished for 3 d to remove all fish from each section before experiments were started. In addition, stream sections between each of the experimental units were electrofished and all fish were moved downstream of the lowest experimental section. Treatments consisted of cutthroat trout only and cutthroat trout + brook trout (n = 3 replicates) and were randomly assigned to the six experimental sections. Trout were stocked on 12 July at a density of 0.5 fish/m^2. This density was the average density for all trout species found in Gilbert Creek during the summer of 1992 (P. Cavalli, *personal communication*). Cutthroat trout used in the experiment (96-133 mm total length; average = 116.42 ± 1.06 mm) were obtained from

nearby Steel Creek and brook trout (95-135 mm; average = 115.46 ± 1.25 mm) were taken from Gilbert Creek. Fish were individually marked with visual implant tags, so that individual growth, lipid levels, and diets could be monitored throughout the experiment. Trout were measured to the nearest 0.1 mm and weighed to the nearest 0.01 g before being stocked into the sections.

Individual trout lengths, weights, and diets were sampled on 12 August (30 d after initiation of experiment) by backpack electrofishing. Diets were preserved in 95% ethanol. Prey items were later identified, counted, and measured in the laboratory. To relate fish diets to food availability, drift samples were taken within 1 wk of fish sampling. Drift nets were placed in the interface between the riffle-pool habitat because most trout were observed in the pool habitat (*personal observation*). Drift nets were set in place 1 h before darkness and drift was sampled for approximately 2 h. Drift samples were preserved in 95% ethanol and drifting prey were counted and measured in the laboratory.

Experiments ended on 12 September. Trout were electrofished from the experimental sections and fish lengths and weights were recorded as before. Trout were sacrificed in the field with MS-222 and frozen in liquid nitrogen. Gut contents were later removed in the laboratory for identification, enumeration, and measurement. A drift sample was taken as described above 1 or 2 d prior to the end of the experiment.

Growth Rates.--Growth rates of cutthroat trout were used to determine if brook trout affected cutthroat trout in the field. Growth rate was calculated as a change in

weight ($weight_{final}$ - $weight_{initial}$). A one-way ANOVA was used to determine any significant differences in growth rates between the fish treatment. One of the cutthroat trout- only replicates had to be thrown out for all analyses (growth rates, lipids, and diets) because a very large brook trout (223 mm total length) was electrofished out of the section on 12 August.

Lipid Levels.--For lipid analysis, fish were dried at 60°C for 24 h and weighed to the nearest 0.01 g. Fat was then extracted with petroleum ether using a modification of the procedure described by Bligh and Dyer (1959). The percent fat of the whole fish was determined by dividing total fat grams by the dry weight of the fish (in grams).

Diets.--Diets of cutthroat trout were used to determine if cutthroat trout showed a shift in prey preference when brook trout were present. Diets taken on 12 August and drift sampled 21-23 August were converted to biomass using regression equations (as described previously). Cutthroat trout diets from the last day of the experiment were not analyzed due to inadequate preservation. To determine if cutthroat trout differed in prey preference when brook trout were present, biomass in the diets and drift were compared using Chesson's Alpha (Chesson 1978). One-way ANOVAs were used to analyze Chesson's Alpha for each of the prey categories (Ephemeroptera, Trichoptera, Diptera larvae, other aquatics, and terrestrials) between the treatments. Total biomass was analyzed with a one-way ANOVA. Total biomass was transformed as described previously.

RESULTS

Diet Survey

Cutthroat trout sympatric with brook trout did not differ in prey use or in the time when the prey were consumed when compared to allopatric cutthroat trout. No significant differences in prey use of cutthroat trout were found among fish treatment, time of day, or the interaction for any of the prey groups ($P > 0.10$). There was also no significant difference in the total biomass of prey consumed among the fish treatment, time of day, or the interaction ($P > 0.10$).

Laboratory Feeding Experiment

Encounter and capture rates as well as the total probability of a successful predation event of cutthroat trout were not significantly different among treatments, food positions, or the interaction of the two factors when analyzed as a two-way repeated-measures ANOVA (Table 3, Table 4, and Table 5). Attack rate, however, was significantly different for both treatment and food position, but not for the interaction (Table 3, Table 4, and Table 5). Cutthroat trout attacked significantly more food items per food items encountered (0.49 ± 0.044 [mean ± SE]) in the absence of brook trout than in the presence of brook trout (0.34 ± 0.051). Cutthroat trout also attacked significantly more food items that were released from the middle of the water column (0.57 ± 0.044 [mean ± SE]) than food items released from the surface (0.26 ± 0.050).

Results from a chi-square analysis suggest that there were no significant

differences in the frequency of location of cutthroat trout (middle or bottom of the tank) between the two treatments ($\chi^2 = 0.173$, df = 1, $P > 0.10$).

Enclosure Experiment

Growth Rates.--Growth rate was not significantly different between treatments ($F = 1.48$, df = 1,3, $P = 0.3110$); however, there was a trend of higher growth rates for the cutthroat trout-only treatment (4.07 ± 0.953 g [mean ± SE]) than for the cutthroat trout with brook trout (2.58 ± 0.777 g).

Lipid Levels.--Lipid levels of cutthroat trout were significantly higher in the absence of brook trout ($t = 2.4495$, df = 3, $P = 0.0917$, 0.18 ± 0.001 [mean ± SE]) than in the presence of brook trout (0.15 ± 0.009).

Diets.--Cutthroat trout did not differ in preferences for prey items when brook trout were present. No significant differences in diet electivity by cutthroat trout were found between treatments for any of the prey groups ($P > 0.10$, Figure 1). The total biomass of prey consumed also did not differ between the treatments ($P > 0.10$).

DISCUSSION

Most investigations of competitive interactions between salmonids have focused on microhabitat shifts of one or more species in allopatric versus sympatric situations (Hartman 1965, Griffith 1972, Fausch and White 1981, Cunjak and Green 1984, Larson and Moore 1985, Glova 1986, 1987, Hearn and Kynard 1986, Kennedy and Strange

1986, Hindar et al. 1988, Fraser and Power 1989, DeWald and Wilzbach 1992, Lohr and West 1992). This study focused on how the feeding, growth, and possibly the survivorship of cutthroat trout were affected by the presence of brook trout and the competitive mechanism responsible for those effects.

Results from the laboratory experiment suggest that the feeding efficiency of cutthroat trout declined in the presence of brook trout. The decline in feeding efficiency was in the form of decreased attack rates of cutthroat trout when brook trout were present. Attack rates and the total probability of a successful predation event were found to be significantly lower for surface prey than for midwater prey. This result might be explained by trout preferring to feed on drift rather than surface food items or perhaps the fish felt more vulnerable to aggressive attacks by the other fish when food was released as surface prey. It should be noted that the decrease in feeding efficiency of cutthroat was not due to the fact that brook trout attacked and consumed most food items (average feeding efficiency of brook trout, encounter = 0.02 ± 0.003, attack = 0.44 ± 0.064, capture = 0.73 ± 0.070, total probability = 0.02 ± 0.019), resulting in prey depletion, but rather cutthroat trout were less aggressive in the presence of brook trout, resulting in fewer attempts to attack food items. While aggressive attacks of one fish on another were never frequent enough to quantify during feeding trials, almost all aggressive acts noted were from brook trout on cutthroat trout.

Other studies have shown decreased feeding efficiency of native salmonids in the presence of exotic competitors. DeWald and Wilzbach (1992) found that prey capture rates of native brook trout declined in the presence of brown trout. Their

finding of decreased prey capture rates was due to a behavioral shift of brook trout in the presence of brown trout. In this study, cutthroat trout almost always remained inactive and were typically positioned behind brook trout. However, when a cutthroat trout was paired with another cutthroat trout, both fish actively fed and moved throughout the experiment. The change in behavior of cutthroat trout in the presence of brook trout probably resulted in a decreased feeding efficiency. This behavioral shift could be the reason growth rates and lipid levels of cutthroat trout declined in the presence of brook trout in the field experiment. Dominant trout have previously been shown to grow faster and more efficiently and have higher lipid levels (Li and Brocksen 1977). In a study looking at intraspecific competition of rainbow trout for space, Li and Brocksen (1977) showed that dominant trout had an average fat content of 15%, whereas subordinate trout only had an average of 10% fat. Rose (1986) showed a decrease in the growth rate of subyearling brook trout after the emergence of rainbow trout. However, Rose (1986) did not have an allopatric control for comparison with sympatric rainbow trout. Although the above studies have shown how negative interactions reduce growth rates of salmonids in the field and in the laboratory, not all interactions between salmonids have resulted in negative results. In a study with brown trout, Kocik and Taylor (1994) found that interactions with steelhead did not have any negative effects on the growth or survival of brown trout.

The field enclosure study showed that the presence of brook trout resulted in significantly decreased fat levels and slightly lower growth rates of cutthroat trout in their natural environment. The nonsignificant result of growth rates may be misleading,

wever, because the power for the analysis was only 0.12. It was also discovered that one of the cutthroat trout + brook trout replicates differed greatly from the other two replicates (growth rate means for replicate 1 = 1.84 g, replicate 2 = 1.76 g, and replicate 3 = 4.13 g). It is suspected that higher temperature in replicate 3, due to less overhanging riparian vegetation, is the reason for this outlier. Decreased growth and fat levels could have negative effects on the overwinter survivorship of cutthroat trout. Overwinter survivorship has been shown to be higher for larger fish than for smaller fish and is probably the result of higher levels of energy storage (Smith and Griffith 1994). Cunjak and Power (1987) showed that despite continued feeding in the winter, the condition factors of brook trout and brown trout decreased significantly in the early winter and remained low until the onset of spring. They suggested that the decreased condition factors were the result of an early-winter depletion of lipid reserves. Any decrease in the accumulation of lipid reserves prior to the onset of winter may contribute to the inability of cutthroat trout to survive long, cold winters.

Lower growth rates and fat levels may also have negative effects on the reproductive output of cutthroat trout. Because cutthroat trout in the Uinta mountains may have a relatively short, summer growing season, decreased growth rates may prevent cutthroat trout from reaching sexual maturity as early as they could if brook trout were not present. Because lipid reserves are important for the reproductive energy budget in fish (Meffe and Snelson 1993), cutthroat trout may not have adequate energy reserves for springtime reproduction, especially if those reserves are spent trying to survive a long winter.

The decreased fat levels of cutthroat trout observed in the field are most likely the result of interference competition. Diets taken from the field experiment and from the previous summer did not show any differences in prey use of cutthroat trout in the presence of brook trout. If exploitative competition were important, one might expect to see a difference in the types or amounts of prey consumed, or a difference in the time at which prey were consumed by cutthroat trout in the presence of brook trout. Griffith (1974) showed that subyearling and older cutthroat trout differed little in food preferences, independent of whether they lived allopatrically or sympatrically with brook trout. Interference competition is the most likely mechanism responsible for negative interactions between the two salmonids because there were no differences in prey use or differences in the amount of prey consumed in the field and because laboratory experiments implied a behavioral shift in cutthroat trout when brook trout were present. We caution, however, that diets and food availability could only be analyzed for one day in the stream survey and in the field enclosure experiment, because we did not want to stress the fish by sampling more often and because the diets from the end of the experiment were not preserved properly.

This research focused on interactions between 2+ age fish. It is not known if the interactions seen in this study also occur in other life-stages such as reproducing adults and subyearling cutthroat trout, but effects on subyearling cutthroat trout may be especially severe. Subyearling brook trout have been shown to maintain a 20- mm size advantage over cutthroat trout of the same year-class (Griffith 1972), because brook trout fry emerge in the spring and cutthroat trout fry do not emerge until late summer.

The size advantage of subyearling brook trout may produce pronounced negative interactions with subyearling cutthroat trout and, thus, may increase the possibility of higher overwinter mortality and delayed sexual maturity.

Interactions between cutthroat trout and brook trout may also be altered by temperature and gradient in the stream. Brook trout have been found to be more aggressive and consume more food than cutthroat trout at high temperatures of 20°C; however, no differences between the two species were found at 10°C (DeStaso and Rahel 1994). In contrast, Cunjak and Green (1986) found that brook trout were dominate over rainbow trout at both 8 and 13°C, but neither species showed a competitive advantage at 19°C. Gradient has also been suggested to affect the distribution of salmonids in streams. Fausch (1989) noted that cutthroat trout find refuge from brook trout in upstream reaches of streams where physical conditions may be unsuitable for the introduced brook trout.

This study provides evidence for how an introduced species can affect the behavior, growth, and lipid levels of a native species. Because growth and lipid accumulation are important to fish survival, cutthroat trout overwinter survivorship and reproduction may be in jeopardy if brook trout are present. Puckett and Dill (1985) have suggested that for animals in which rapid growth is linked to survival and fitness, a net energy maximizing foraging strategy should be favored (Puckett and Dill 1985). Cutthroat trout in the Uinta mountains may not have efficient foraging strategies when brook trout are present. If so, interference competition with brook trout may be an important mechanism contributing to the decline of Colorado River cutthroat trout.

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TABLE 1. Power analyses for laboratory feeding experiment.

Feeding Efficiency	Two-Way Repeated Measures ANOVA
Encounter Rate	0.10
Attack Rate	0.13
Capture Rate	0.10
Total Probability	0.12

TABLE 2. Habitat descriptions of manipulated stream sections in Gilbert Creek. Means ± 1 SD and ranges for each habitat variable are given below.

Habitat Description	Average	Range
Riffle Length	7.1 ± 1.03 m	5.3 - 9.1 m
Riffle Width	3.4 ± 0.65 m	2.1 - 4.0 m
Pool Length	2.8 ± 0.41 m	2.1 - 3.3 m
Pool Width	3.0 ± 0.55 m	1.8 - 3.6 m
Area	30.8 ± 4.83 m^2	23.7 - 37.3 m^2
Length Between Sections	38.8 ± 23.01 m	12.7 - 86.0 m

TABLE 3. Means and standard errors of feeding efficiency shown for each of the treatment levels for the laboratory feeding experiment.

Source	Treatment	Mean(SE)
Encounter Rate	Cutthroat Only	0.07(0.009)
	Cutthroat + Brook Trout	0.07(0.009)
	Surface Food	0.07(0.009)
	Midwater Food	0.08(0.009)
Attack Rate	Cutthroat Only	0.49(0.044)
	Cutthroat + Brook Trout	0.35(0.051)
	Surface Food	0.26(0.050)
	Midwater Food	0.57(0.045)
Capture Rate	Cutthroat Only	0.88(0.035)
	Cutthroat + Brook Trout	0.83(0.048)
	Surface Food	0.82(0.049)
	Midwater Food	0.90(0.033)
Total Probability	Cutthroat Only	0.04(0.011)
	Cutthroat + Brook Trout	0.04(0.011)
	Surface Food	0.02(0.011)
	Midwater Food	0.05(0.011)

TABLE 4. Means and standard errors of feeding efficiency shown for each interaction of the treatment levels for the laboratory feeding experiment.

Source	Treatment	Mean(SE)
Encounter Rate	Cutt*Surface	0.08(0.012)
	Cutt*Midwater	0.07(0.012)
	Cutt+Brook*Surface	0.06(0.013)
	Cutt+Brook*Midwater	0.09(0.013)
Attack Rate	Cutt*Surface	0.30(0.063)
	Cutt*Midwater	0.67(0.061)
	Cutt+Brook*Surface	0.22(0.077)
	Cutt+Brook*Midwater	0.48(0.065)
Capture Rate	Cutt*Surface	0.81(0.052)
	Cutt*Midwater	0.96(0.046)
	Cutt+Brook*Surface	0.82(0.082)
	Cutt+Brook*Midwater	0.85(0.049)
Total Probability	Cutt*Surface	0.04(0.016)
	Cutt*Midwater	0.04(0.016)
	Cutt+Brook*Surface	0.01(0.016)
	Cutt+Brook*Midwater	0.06(0.016)

TABLE 5. Results from laboratory feeding experiment of cutthroat trout in the presence and absence of brook trout. Fish Treatment (cutthroat trout only/cutthroat + brook trout) and food position (surface/midwater) were the factors used in the analysis.

Feeding Efficiency	Source of Variation	df	F	P
Encounter	Fish Treatment	1,110	0.02	0.88
	Food Position	1,110	0.35	0.56
	Fish*Food	1,110	2.27	0.13
Attack	Fish Treatment	1,95	4.51	0.04
	Food Position	1,95	22.25	0.00
	Fish*Food	1,95	0.66	0.42
Capture	Fish Treatment	1,73	0.72	0.40
	Food Position	1,73	2.17	0.14
	Fish*Food	1,73	0.88	0.35
Total Probability	Fish Treatment	1,110	0.00	0.96
	Food Position	1,110	3.37	0.07
	Fish*Food	1,110	2.20	0.14

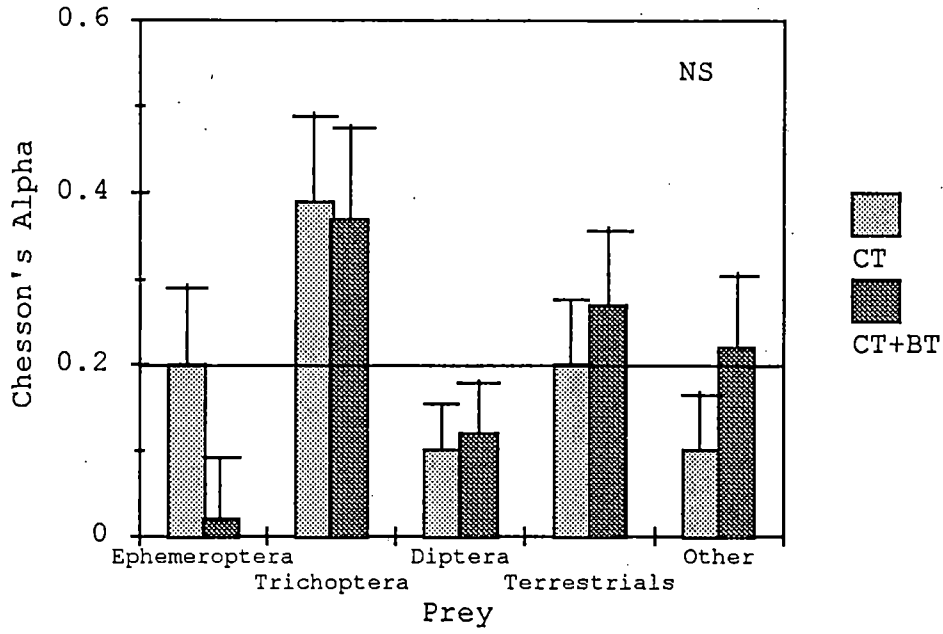

Figure 1. Electivity indices of cutthroat trout with and without brook trout. Solid line indicates neutral selectivity of prey. Means and standard errors are shown.

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